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Contents

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PARASITES OF COD AND OTHER MARINE FISH FROM THE BAIE DE CHALEUR REGION[1]

BY ANITA FOCHS HELLER[2]

Introduction

Stafford (33) was the first to undertake the study of parasites of marine fishes along the Canadian Atlantic coast. However, his paper on the "Trematodes from Canadian fishes" created a confusion in the taxonomic literature owing to his unsatisfactory descriptions. This situation was remedied by Miller (23) who re-examined and re-identified the specimens in Stafford's slide collection. Further work on Canadian fish trematodes was done by Cooper (3). In 1930, Bere (2) published a paper on "The parasitic copepods of the fish of the Passamaquoddy region". On the Pacific coast, trematodes were dealt with by McFarlane (20). Wardle (35, 36, 37) dealt with cestodes and has also considered the Hudson's Bay area. Kuitunen-Ekbaum (12) and Smedley (31) have described nematodes.

However, there is still a lack of knowledge concerning the distribution of known species and it seemed that a further contribution toward this end would be of value. The still insufficient amount of systematic and faunistic information available on the marine parasites of Canada's east coast lends additional interest to their study.

The host species examined in the present survey occur also along the Atlantic coast of the United States and, therefore, the numerous publications of American authors have a direct bearing on the subject.

Because of the circumpolar distribution of the host fishes and their accompanying parasites, it has also been necessary to consult the results of European investigations.

Methods and Procedure

The codfish, skates, and flounders were taken on lines, partly three to four miles out at sea from Grande-Rivière, County Gaspé South, Quebec, Canada, and partly on the Miscou Bank about 30 mi. northeast of Grande-Rivière. The salmon were captured in salmon drift nets four miles out at sea. The

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[2] *Graduate Assistant.*
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herring were fished in drift nets three to four miles from shore and the mackerel were taken, accidentally, both in the salmon and herring nets. The dogfish came from the Miscou Bank, while the smelt were caught in dip nets a short distance up the Grande-Rivière, where they were swimming up river to spawn. The rest of the fish were caught, accidentally, in lobster traps near shore.

The host specimens were examined externally as soon as possible after their capture. The copepods were taken off the gills and skin and from inside the mouth cavity. The trematodes were collected from the gills and the oral cavity and the leeches were found inside the mouth. The body was then split open ventrally and the body cavity, muscles, and mesenteries were examined for nematodes and cestode larvae; the alimentary tract was lifted out from the oesophagus to the rectum, placed in a dish, and slit open. The contents were diluted with isotonic seawater and examined while still alive. The copepods were killed, fixed, and stored in 5% formalin. The leeches, nematodes, and acanthocephalans were killed, and fixed in hot 70% alcohol, and stored in 70% glycerine alcohol. The trematodes and cestodes were killed in hot fresh water and stored in 10% formalin.

In the fall, at the Institute of Parasitology, the trematodes and cestodes were stained, some with Ehrlich's acid haematoxylin, others with Gower's alum carmine. Both methods gave satisfactory results. They were then cleared in beechwood creosote and mounted in Canada balsam.

The Acanthocephala and Nematoda were cleared in lactophenol and examined, unmounted, while in that liquid. All the details, necessary for identification, were clearly visible by that method.

TABLE I

Hosts	Total number examined	Number of host specimens parasitized by:					
		Acanthocephala	Trematoda	Cestoda	Nematoda	Copepoda	Hirudinea
Acanthocottus scorpius (Shorthorn sculpin)	1	—	1	—	1	—	—
Clupea harengus (Herring)	27	—	11	—	2	—	—
Gadus callarias (Cod)	440	53	40	18	440	277	—
Microgadus tomcod (Tomcod)	1	1	1	—	1	—	—
Osmerus mordax (Smelt)	4	—	3	—	2	—	—
Pseudopleuronectes americanus (Winter flounder)	3	—	2	1	1	—	—
Salmo salar (Salmon)	5	—	3	4	2	4	—
Scomber scombrus (Mackerel)	3	—	—	—	3	—	—
Tautogolabrus adspersus (Cunner)	2	—	—	—	1	—	—
Urophycis chuss (Squirrel hake)	2	—	—	—	2	—	—
Zoarces anguillaris (Eelpout)	2	—	—	—	—	—	1
Raja erinacea (Summer skate)	2	—	—	2	2	—	—
Raja scabrata (Prickly skate)	20	—	1	13	1	2	—
Raja stabuliforis (Barndoor skate)	1	—	—	1	—	—	—
Squalus acanthias (Spiny dogfish)	3	—	—	—	—	—	—

Some of the Copepoda were removed from the formalin, washed, dehydrated, and cleared in lactophenol. Some specimens were washed and then heated in 10% sodium hydroxide in a water-bath so that the soft tissue was removed and only the chitinous structures remained. This latter procedure was used when a dissection of the mouth parts had to be carried out.

Results

(1) General

The accompanying table (Table I) shows how many specimens of each of the 15 host species were examined, as well as the number of these that were parasitized by the different groups of helminths or copepods.

(2) Helminths

A. Trematoda

Podocotyle atomon (Rudolphi, 1802) Odhner, 1905

Hosts: Acanthocottus scorpius, Gadus callarias, Pseudopleuronectes americanus
Habitat: Alimentary tract, mainly intestine
Incidence and abundance: Sculpin —June 17, 1947, 3 specimens from 1 fish
Cod —June 30, 1947, 1 specimen from 1 fish
Flounder—June 11, 1947, 2 specimens from 1 fish
June 28, 1947, 4 specimens from 1 fish

Discussion

The specimens from the three hosts agreed with the descriptions of *Podocotyle atomon* of Odhner (25), Manter (21), Linton (16), and Miller (23) in most fundamental respects and they were therefore referred to this species. The only characteristic causing some difficulty was the position of the vitellaria. All descriptions of *P. atomon* mention the fact that the vitellaria run laterally in an unbroken line and do not come together between the testes. Most of the material that was examined, however, although agreeing in the first point, does have vitellaria filling the intertesticular space to a varying extent.

This fact has been observed before by various authors. Linton (16) stated: "In some cases there is little or no interval between the testes, in others there is an interval into which follicles of vitellaria are inserted". Manter (21) also mentioned a case where the vitellaria approach each other and he considered the oesophagus length to be the best characteristic. Park (26) found that the distribution of the vitellaria varies widely within a given species.

Dawes (6) emphasized the fact that *Podocotyle atomon* is a very variable species and voiced the opinion that "several species which occur outside Europe will certainly prove to be invalid, and the same might be said of some European forms".

During the present investigation, it was observed, while trying to orientate a specimen of *Podocotyle atomon* from *Pseudopleuronectes americanus* between

the slide and the cover slip under the microscope, that a slight pressure brought to bear accidentally on the trematode caused the yolk follicles to be pushed into the intertesticular space. This is interesting in connection with Nicoll's statement (24) "that artefacts produced by inappropriate methods of fixation modify specimens so that they answer to the descriptions of other species".

Miller (23), in re-examining Stafford's slide material, created the new species *Podocotyle staffordi* from *Gasterosteus aculeatus* (stickleback). One of the distinctive characteristics of this new species was said to be the fact that "*P. staffordi* has the vitellaria filling the intertesticular space but, unlike *P. olssoni*, the vitellaria are not discontinued laterally in the region of the testes".

The opportunity was afforded to examine that same slide material and in one specimen, labelled *Podocotyle atomon* from *Acanthocottus scorpius*, the yolk glands came together between the testes and were continuous laterally.

From the table (Table II) comparing the measurements of Miller's *P. atomon* and *P. staffordi* with the *P. atomon* collected during the present investigation, it would appear that there is a general overlapping of characteristics and that all the specimens belong to the highly variable species, *P. atomon*.

TABLE II

	P. atomon, Miller's material	*P. staffordi*, Miller's material	*P. atomon*, present material
Total length	1.45 to 3.81 mm.	1.07 to 1.57 mm.	4.33 mm.
Relation of length to width	1 : 4, 1 : 3	1 : 5, 1 : 6	1 : 6
Oesophagus length in relation to pharynx length	As long or longer than pharynx	Somewhat longer than pharynx	Longer than pharynx
Testes	½ width of body	½ width of body	A little less than ½ width of body
Vitellaria	Continuous laterally, do not fill intertesticular space	Continuous laterally, fill intertesticular space	Continuous laterally, fill intertesticular space

Podocotyle reflexa (Creplin, 1825)

Host: Microgadus tomcod

Habitat: Intestine

Abundance: June 11, 1947, 3 specimens from 1 fish

Discussion

The material at hand agreed in most points with Odhner's description, with testes occupying almost the whole body width and a relation of the length of the body to its width as 1 to 10.

However, the cirrus sac reached just halfway the distance from the acetabulum to the ovary and Odhner (25) mentioned that aspect as a characteristic of *P. olssoni.* Miller (23) found this same condition in a specimen from the hake.

Furthermore the oesophagus length of the present specimens equals that of the pharynx, another feature of *P. olssoni.*

The material was assigned to *P. reflexa* with some doubt, especially since the same fish contained specimens that were identified as *P. olssoni.* There is a possibility that differential degrees of contraction caused them to assume a misleading appearance.

Dawes (6) quoted Nicoll (24) as finding "that variability affects certain characters upon which Odhner depended for the determination of *P. reflexa* e.g. shape, flattening, relative position of the suckers", and also mentioned that *P. reflexa* and *P. olssoni* may be identical with *P. atomon.*

Podocotyle olssoni Odhner, 1905

Host: Microgadus tomcod

Habitat: Intestine

Abundance: June 11, 1947, 3 specimens from 1 fish

Discussion

The material was found in association with *P. reflexa* in a tomcod and there may be a possibility that it represents strongly contracted specimens of the latter species or that *P. reflexa* specimens belong really to *P. olssoni.* In the discussion of *P. reflexa*, the possibility of assigning *P. reflexa* and *P. olssoni* to *P. atomon* was also mentioned.

Steringophorus furciger (Olsson, 1868)

Host: Pseudopleuronectes americanus

Location: Alimentary tract

Abundance: June 28, 1947, 4 specimens from 1 fish

Discussion

The specimens were typical *Steringophorus furciger* according to the description of Linton (16), Miller (23), and Dawes (6).

Otodistomum cestoides (Beneden, 1870)

Host: Raja scabrata

Habitat: Intestine

Abundance: Aug. 29, 1947, 1 specimen from 4 fish

Discussion

The trematode was obviously immature so that neither the eggs nor the genital papillae could be measured and it was assigned to *Otodistomum cestoides* rather than *O. veliporum* purely on the basis of its distribution.

Van Cleave and Vaughn (34) maintained "that the American forms comprise a single highly variable species to which the name *Otodistomum cestoides* should be applied".

Dawes (6) felt that if the egg size of two of the subspecies of Dollfus varied to such an extent as was shown by Van Cleave and Vaughn, "then the remaining subspecies are invalidated" and "it seems logical to conclude that a single species of the genus *Otodistomum* infects cartilaginous fishes all over the world, and that it should be known not as *O. cestoides* but as *O. veliporum*.

Although this conclusion seems logical, the problem is still in an unsettled condition and the present species was, for the time being, identified as *O. cestoides*.

Brachyphallus crenatus (Rudolphi, 1802)

Hosts: Clupea harengus, Osmerus mordax, Salmo salar

Habitat: Stomach and remainder of digestive tract in the herring and smelt. One specimen was found on the gills of salmon. It may be noted here that trematodes frequently migrate from the alimentary tract to the gills in fish that have been dead for some time.

Incidence and abundance:

Herring—	July 28, 1947,	23 specimens from	11 fish
	July 31, 1947,	19 specimens from	5 fish
	Aug. 18, 1947,	6 specimens from	5 fish
Smelt —	June 11, 1947,	1 specimen from	3 fish
	June 20, 1947,	54 specimens from	1 fish
Salmon—	June 30, 1947,	1 specimen from	1 fish

Discussion

The specimens met with in this investigation were typical *Brachyphallus crenatus* with lobed vitellaria and a well defined presomatic pit.

This species was first recorded from America by Lander (13), from *Osmerus mordax*, who described its anatomy in detail under the name *Hemiurus crenatus.*

The typical condition of the vitellaria of *Brachyphallus crenatus* was found in the present material, agreeing with the observations of Lloyd (17), Manter (21), and Linton (16) regarding the American forms of the species.

Hemiurus levinseni Odhner, 1905

Host: Gadus callarias

Habitat: Alimentary tract

Abundance:

July 16, 1947,	6 specimens from	100 fish
July 24, 1947,	22 specimens from	31 fish
Aug. 3, 1947,	8 specimens from	12 fish
Aug. 8, 1947,	30 specimens from	21 fish
Aug. 13, 1947,	5 specimens from	100 fish

Discussion

The present material was determined as belonging to *H. Levinseni* by consulting Odhner's (25) description.

Lecithaster confusus Odhner, 1905

Host: Osmerus mordax

Habitat: Stomach

Abundance: June 20, 1947, 1 specimen from 1 fish

Discussion

Lühe's (18) and Linton's (16) descriptions were used in the identification. The main problem was to differentiate *Lecithaster confusus* from *L. gibbosus.*

Lühe (18) used the position of the seminal vesicle in relation to the ventral sucker as a characteristic, stating that it extends behind the ventral sucker in *L. confusus* but not *L. gibbosus.* He also mentioned the shape of the ovary as being rounded in *L. gibbosus* and longish in *L. confusus.*

Neither the seminal vesicle nor the ovary could be distinguished clearly in the single available specimen. However, the lobes of the vitellaria were short and scarcely as long as broad, agreeing with Lühe's description. Furthermore, the measurements placed the present material in the species *L. confusus.*

Derogenes varicus (*Müller, 1784*)

Hosts: Gadus callarias, Osmerus mordax, Salmo salar

Habitat: Gills, stomach. As was mentioned before in considering *Brachyphallus crenatus,* the location of a digenetic trematode on the gills of a fish is probably due to the migration of the parasite from the alimentary tract following the death of the host.

Incidence and abundance:	Cod —July 24, 1947,	11 specimens from	31 fish
	Aug. 4, 1947,	15 specimens from	12 fish
	Aug. 8, 1947,	37 specimens from	21 fish
	Aug. 11, 1947,	13 specimens from	10 fish
	Aug. 13, 1947,	18 specimens from	100 fish
	Smelt —June 30, 1947,	36 specimens from	1 fish
	Salmon—July 3, 1947,	18 specimens from	1 fish

Discussion

This was by far the most abundant species of trematode encountered, occurring in large numbers in the parasitized host specimens, often giving the stomach lining a yellow appearance by their presence. Manter (21) mentioned that it occurred in many host species but in small numbers, but this does not seem to be the case in the present material. The incidence given above for this case is misleading since only representative samples were collected. The specimens agreed with Odhner's (25) and Dawes (6) descriptions.

B. Cestoda

Phyllobothrium dagnalli Southwell, 1927

Hosts: Raja scabrata, Raja stabuliforis

Habitat: Stomach, spiral valve, intestine

Incidence and abundance: Prickly skate—Aug. 25, 1947, 2 specimens from 4 fish
Aug. 29, 1947, 4 specimens from 3 fish
Aug. 30, 1947, 1 specimen from 5 fish
Barndoor skate—Aug. 27, 1947, 3 specimens from 1 fish

Discussion

The material agreed fully with the description of *P. dagnalli* of Southwell (32) from Ceylon.

Anthobothrium cornucopia van Beneden, 1850

Host: Raja scabrata

Habitat: Stomach, spiral valve, intestine

Abundance: Aug. 25, 1947, 2 specimens from 4 fish
Aug. 29, 1947, 3 specimens from 3 fish
Aug. 30, 1947, 24 specimens from 5 fish

Discussion

According to the keys of Joyeux and Baer (9), the material appeared to belong to the species *Anthobothrium cornucopia*. However, the description in "Cestodes de France" is very short. Southwell (32) considered the genus *Anthobothrium* to be included in the genus *Phyllobothrium* but did not mention the type species *A. cornucopia*.

The drawing of Fuhrmann (8) of a scolex of *A. cornucopia* from *Galeus canis* seems to show a myzorhynchus and no loculi as in the case of the present specimen. Fuhrmann gave the length of the cestode as 20 cm. but the material at hand corresponds rather with Joyeux and Baer's measurements, 10–252 mm.

Scyphophyllideum giganteum (van Beneden, 1859)

Host: Raja scabrata

Habitat: Intestine

Abundance: Aug. 29, 1947, 1 specimen from 3 fish
Aug. 30, 1947, 2 specimens from 5 fish

Discussion

These specimens belonging to the species *Scyphophyllideum giganteum* differ from all other Phyllobothriidae in having enormous globular bothridia, which have the appearance of suckers such as are found in the Cyclophyllidea. They were identified by consulting Woodland (40) and Joyeux and Baer (9).

Echinobothrium raji n. sp.

(Figs. 1 and 2)

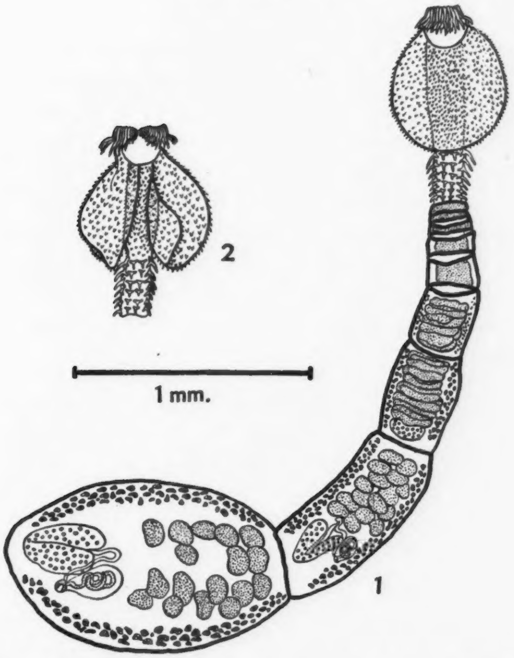

FIG. 1. *Echinobothrium raji* n. sp. entire worm, ventral view.

Fig. 2. *Echinobothrium raji* n. sp. scolex, lateral view.

Host: Raja scabrata

Habitat: Stomach, spiral valve

Abundance: Aug. 25, 1947, 21 specimens from 4 fish
Aug. 29, 1947, 1 specimen from 3 fish

Description: The length of the cestodes with seven proglottids is about 3 mm. Often eight or nine proglottids are present, depending at what stage the ripe segments detach themselves. The scolex measured to the base of the cephalic peduncle ("Kopfstiel") is 0.850 mm. long and the head, including the rostrum and "neck" but not the armed portion ("Kopfstiel") measures 0.675 mm. in length. The "neck" has a width of 0.195 mm. and a length of 0.480 mm. The rostrum with a diameter of 0.150 mm. bears, on either side, groups of 30 to 32 hooks arranged in two rows. On each side of the big hooks there are six small hooks. Each large hook is 0.113–0.120 mm. long and the small hooks decrease in size going toward the edge of the cluster. There are no

spines on the base of the rostrum, but some small ones are found on the "neck", which is overhung by two lappets or pseudobothridia. The latter are also covered by minute spines and measure 0.605 mm. in length and 0.540 mm. in width. The cephalic peduncle bears eight longitudinal rows of eight hooks each. These hooks are directed backwards and diminish in length going toward the posterior end. The longest of these hooks are 0.024 mm. long and they are all anchored to the body by a triradiate base. Following the cephalic peduncle, there are three to four immature proglottids wider than long, but increasing in length toward the posterior end of the worm. The first few immature segments show hardly any structure but in the last ones the genital organs are seen. These mature proglottids increase in size becoming longer than wide and the last attached one measures approximately 1.2 mm. in length and 0.525 mm. in width. The cirrus is covered by spines and situated in a cirrus sac opening in the posterior third of the segment. The vagina opens next to the cirrus sac and leads to the U-shaped ovary situated in the posterior end of the segment. There are about 16 testes, which are square in the first proglottids and gradually assume a round shape. The yolk follicles fill the lateral space and the eggs are 0.013 mm. by 0.018 mm., bluntly rounded at one end and pointed at the other.

Discussion

Of the four species described briefly by Joyeux and Baer (9) and in greater detail by Pintner (27), the present species differs from *E. affine* Diesing in size, in the greater number of rostral hooks, and the smaller number of hooks on the cephalic peduncle as well as in the greater number of testes; from *E. brachysoma* Pintner in size, in the number of rostral hooks, hooks on the cephalic peduncle, and number of testes, as well as in the arrangement of the eggs; and from *E. typus* van Beneden in the number of rostral hooks, as well as the number of hooks on the cephalic peduncle and the number of testes.

E. musteli Pintner resembles the present species more closely than the other three, but it differs in having small spines on the base of the rostrum, in the larger number of hooks on the cephalic peduncle, and in the larger number of testes. But *E. raji* and *E. musteli* resemble each other in having nearly the same number of hooks on the rostrum and in the relatively great length of the scolex compared to the rest of the body.

Southwell (32) cited van Beneden's description of *E. typus* and concluded that his own *E. boisi* Southwell, 1911, was synonymous with *E. typus*. He further described *E. affine* and a curious species *E. rhinoptera* Shipley and Hornell, 1906, of which he said: "The two points in which this cestode differs from the other members of the genus, e.g. *E. affine*, *E. typus*, *E. brachysoma* and *E. musteli* are the complete absence of any spines on the head and the

presence of a naked region or "neck" between the head and the armed region of the body" but Southwell added that the head hooks were probably lost. *E. longicolle* Southwell, 1925, described by its discoverer (32) has 180 hooks in each anteroposterior row of the "Kopfstiel".

Tentacularia coryphaenae Bosc. 1802

Host: Salmo salar

Habitat: Body cavity

Abundance: June 30, 1947, 2 specimens from 1 fish

Discussion

The two specimens, at the postlarval stage, were found moving around freely in the body cavity of a salmon. They were off-white and looked like portions of the caeca.

Dollfus (7) cited the opinion of Leuckart, von Siebold, and Pintner in favor of identifying *T. coryphaenae* with *T. quadrirostris*, and stated: "Ce nom (*T. coryphaenae*) a été établi pour la post-larve (ou larve) trouvée par Bosc chez *Coryphaena*; il est postérieur au nom spécifique donné par Goeze à la post-larve (ou larve) trouvée par Goeze chez *Salmo*; j'estime à peu près certain que *quadrirostris* et *coryphaenae* sont la même espèce, mais je n'ai pu me procurer, pour vérification, de spécimens trouvés chez des *Salmo*; je conserve donc, provisoirement, le nom spécifique *coryphaenae*; lorsqu'il sera formellement établi qu'il n'existe aucune différence spécifique, il faudra abandonner définitivement *coryphaenae* au profit de *quadrirostris*."

The present specimens from *Salmo* seem to be fully in agreement with Dollfus' description of *T. coryphaenae*, from *Coryphaena* giving support to the establishment of the name *T. quadrirostris*, which has priority. To be certain however, one would have to be able to compare actual specimens from *Coryphaena* and *Salmo*, especially in respect to the size and arrangement of proboscis hooks.

Grillotia sp. (W. Kahl, 1937)

Host: Raja scabrata

Habitat: Spiral valve, intestine

Abundance: Aug. 25, 1947, 10 specimens from 4 fish
Aug. 30, 1947, 2 specimens from 5 fish

Discussion

The material has all the characteristics of *Grillotia* sp. including the median insertion of the retractor in the proboscis sheath, and the homogeneous armature of the proboscis. The proboscis hooks also correspond to the detailed drawing of Dollfus (7).

Abothrium gadi van Beneden, 1871

Host: Gadus callarias

Habitat: Pyloric caeca, intestine

Abundance:	June 25, 1947,	1 specimen	from	34 fish
	June 30, 1947,	1 specimen	from	1 fish
	July 7, 1947,	3 specimens	from	15 fish
	July 16, 1947,	1 specimen	from	100 fish
	July 24, 1947,	4 specimens	from	31 fish

Discussion

The specimens from cod were determined as *Abothrium gadi* according to Joyeux and Baer (9).

Eubothrium crassum (Bloch, 1779)

Host: Salmo salar

Habitat: Pyloric caeca, intestine

Abundance:	June 18, 1947,	1 specimen	from	1 fish
	June 20, 1947,	1 specimen	from	1 fish
	June 30, 1947,	3 specimens	from	1 fish
	July 3, 1947,	2 specimens	from	1 fish

Discussion

The material was found to be identical with *Eubothrium crassum* as discussed by Wardle (35, 36), Kuitunen-Ekbaum (12), and Joyeux and Baer (9). Cooper (4) considered the same species under the name *Abothrium crassum.*

Diplocotyle olrikii Krabbe, 1874

Host: Pseudopleuronectes americanus

Habitat: Intestine

Abundance: June 28, 1947, 17 specimens from 1 fish

Discussion

The present material was referred to the species *Diplocotyle olrikii* by consulting Wardle's (35, 36) description. Cooper (4, 5) described similar specimens under the name *Bothrimonus intermedius.* Cooper, 1917 and Wardle's (35, 36) comment on this point was: "The species appears to be essentially a parasite of salmonoid fishes. The material described by Schneider, by Nybelin, and by Cooper was taken from pleuronectid fishes, which are probably abnormal hosts. The creation of separate species for such abnormally located specimens of *D. olrikii* purely on the basis of differences from Krabbe's description, seems to me unjustifiable".

In the specimens examined in this study, the two bothridial apertures are always distinctly separate.

C. Acanthocephala

Echinorhynchus gadi Miller, 1776

Hosts: Gadus callarias, Microgadus tomcod

Habitat: Intestine

Incidence and abundance:

Cod	—June 20, 1947,	1 specimen	from	1 fish
	June 30, 1947,	63 specimens	from	1 fish
	July 7, 1947,	44 specimens	from	15 fish
	July 16, 1947,	25 specimens	from	100 fish
	July 21, 1947,	13 specimens	from	24 fish
	July 24, 1947,	38 specimens	from	31 fish
	Aug. 4, 1947,	17 specimens	from	12 fish
	Aug. 5, 1947,	16 specimens	from	9 fish
	Aug. 8, 1947,	18 specimens	from	21 fish
	Aug. 11, 1947,	.6 specimens	from	10 fish
Tomcod	—June 11, 1947,	44 specimens	from	1 fish

Discussion

Lühe's (19) and Markowski's (22) descriptions and drawings referred the present material to the species *Echinorhynchus gadi.*

D. Nematoda

Porrocaecum sp. larvae

Host: Gadus callarias

Habitat: Muscles, body cavity

Abundance: The abundance of this and the following nematode species is not given since it would only be misleading. Representative samples only were collected since the total amount of parasites present was too great.

Discussion

All the larval forms with an intestinal caecum and a ventriculus were determined as belonging to the genus *Porrocaecum.* Some of the smaller larvae without caeca may also have belonged to this genus since according to Baylis (1): "The caecum of this type of larva (*Porrocaecum*) is only developed gradually during its sojourn in the fish host, and the young larvae, before its development, cannot be distinguished with any certainty from those of *Anisakis*".

Baylis (1) and Punt (28) both questioned Kahl's (11) and Wülker's (41) ability to identify specifically larval stages of ascarids in marine fishes and gave excellent reasons to disregard Kahl's and Wülker's identification.

Contracaecum aduncum (Rudolphi, 1802)

Hosts: Gadus callarias, Tautogolabrus adspersus, Microgadus tomcod, Salmo salar, Acanthocottus scorpius, Pseudopleuronectes americanus, Scomber scombrus

Habitat: Stomach, intestine, body cavity, muscles

Discussion

Adults as well as larvae of *Contracaecum* were found. The larvae could not be identified specifically but the possession of an intestinal as well as an oesophageal caecum clearly placed them in the genus *Contracaecum*; and it seems very probable that they belong to the species *C. aduncum* since they were found in the same host specimens as the adults of that species. The adults were determined as being *C. aduncum* by referring to the illustrated descriptions of Kahl (10), Punt (28), and Markowski (22).

Kahl (10), as well as most authors, recorded this nematode under the name *C. clavatum* but Punt (28) in reviewing the literature remarked that no author after *A. Schneider* saw all the species of *Contracaecum* one beside the other and, as a consequence, many synonymous names appeared. Punt also stated that the specific diagnosis of these species is based on the structure of the lips, but that a detailed comparative study of the literature as well as of actual material did not reveal any significant differences between many forms. He drew up a list of synonyms, including *C. clavatum*, to be replaced by the name *C. aduncum*, which has priority. The arguments of Punt seem very convincing and the present material was, therefore, determined to belong to the species *Contracaecum aduncum*.

Eustoma rotundatum (Rudolphi, 1819)

Host: Raja erinacea

Habitat: Stomach, spiral valve

Abundance: Aug. 15, 1947, 11 specimens from 2 fish

Discussion

The present specimens were identified according to the description and drawings of Punt (28) with which they agreed in all respects. Linton (15) gave an illustration of the same species under the name *Ascaris rotundatus*.

Anisakis sp. larvae

Hosts: Gadus callarias, Clupea harengus, Microgadus tomcod, Salmo salar, Osmerus mordax, Urophycis chuss, Scomber scombrus

Habitat: Stomach, intestine, body cavity

Discussion

The larval forms, possessing a ventriculus but lacking caeca, were referred to this genus. Some of these may really represent young forms of *Porrocaecum*

and this question has been discussed when considering the larvae of *Porrocaecum.*

(3) ANTHROPODS

A. COPEPODA

Caligus curtus Müller

Host: Gadus callarias

Habitat: Outside surface

Abundance: Almost all cod examined had these copepods on their skin. The total number per fish could not be determined accurately since the cod had usually been stored for some time in the hold of a ship and been handled extensively before examination, causing many external parasites to become detached. The average number per fish seemed to be 5 to 10 parasites.

Discussion

Both the males and the females were encountered and corresponded to Wilson's (39) description.

Lepeoptheirus salmonis (Kröyer)

Host: Salmo salar

Habitat: External surface

Abundance: On every salmon examined. Many were undoubtedly rubbed off during handling of the fish and therefore the total number per fish could not be recorded.

Discussion

T. and A. Scott's (29, 30) account of the species was consulted and led to its diagnosis. Both males and females were found.

Lernaeocera branchialis (Linnaeus)

Host: Gadus callarias

Habitat: Gill arches

Abundance: June 25, 1947, 1 specimen from 34 fish
June 30, 1947, 1 specimen from 1 fish
July 3, 1947, 1 specimen from 10 fish

Discussion

All three specimens that were found were females. Wilson (39) and T. and A. Scott (29, 30) gave excellent descriptions and illustrations of this species.

Charopinus cameroni n. sp.

(Figs. 3 and 4)

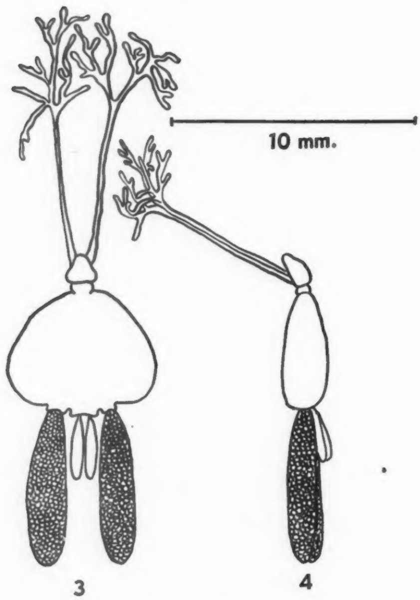

FIG. 3. *Charopinus cameroni* n. sp. dorsal view.

FIG. 4. *Charopinus cameroni* n. sp. lateral view.

Host: Raja scabrata

Habitat: External surface

Abundance: July 16, 1947, 2 specimens from 1 fish
Aug. 25, 1947, 2 specimens from 4 fish
Aug. 30, 1947, 5 specimens from 5 fish

Description

Female

The head is almost triangular in dorsal view and is inclined forwards or ventrally at a 45° angle. This is followed by a short neck, narrower than the base of the head and consisting of a single segment. The trunk is relatively plump, much wider than the head and almost oval, with the longer axis directed sideways. The posterior end of the trunk is emarginated and bears the egg sacs and posterior processes. The egg sacs are quite plump and long, being twice the length of the trunk. The posterior processes are situated dorsal to the egg sacs.

(Figs. 5, 6, 7, 8 and 9)

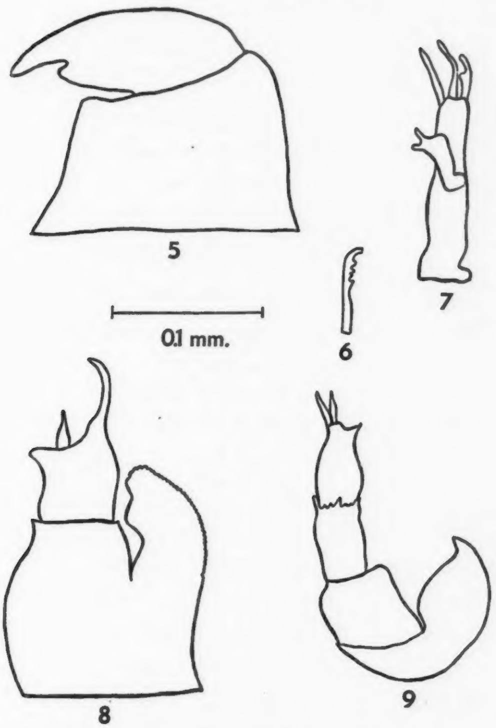

FIG. 5. *Charopinus cameroni* n. sp. maxilliped.

FIG. 6. *Charopinus cameroni* n. sp. mandible.

FIG 7. *Charopinus cameroni* n. sp. first maxilla.

FIG. 8. *Charopinus cameroni* n. sp. second antenna.

FIG. 9. *Charopinus cameroni* n. sp. first antenna.

The first antenna is four-jointed and bears two terminal spines as well as several spines at the joint between the last and penultimate segment. The second antenna is almost chelate with a curved exopod, having a dentate margin and a jointed endopod. The endopod has two terminal spines. The first maxilla is tipped with three large setae and bears a bifid palp. The second maxillae are somewhat longer than the body, excluding the egg sacs. There is no bulla and the ends of each maxilla ramify throughout the host tissue. The mandibles are narrow and long and bear a small number of coarse teeth. The maxillipeds are very stout and chelate, with a curved second joint articulating at right angles to the first joint.

No males were found.

Measurements: Average female specimen

	Total length	2 cm. (including egg sacs)
	Cephalothorax	2 mm. length
		3 mm. width (maximum)
	Neck	0.75 mm. length
	Trunk	5 mm. length
		7 mm. width
	Posterior processes	2 mm. length
		0.7 mm. width
	Egg sacs	1 cm. long
	First antenna	0.180 mm. long, 0.120 mm. wide at base
		0.040 mm. wide at tip
	Second antenna	0.135 mm. wide at base
		0.125 mm. long
	First maxilla	0.150 mm. long, 0.037 mm. wide
	Second maxilla	8 mm. long
	Maxilliped, 1st joint	0.195 mm. wide
		0.170 mm. long
	2nd joint	0.150 mm. long
		0.075 wide
	Mandible	0.060 mm. long
		0.0075 mm. wide

Discussion

The present species belongs to the genus *Charopinus* Kröyer as defined by Wilson (38), the most striking feature being the lack of a bulla, a character which differentiates it, among others, from the genus *Lernaeopodina*. Wilson described the cephalothorax as being bent dorsally but T. and A. Scott (29, 30) show *Charopinus* (*Lernaeopoda*) *cluthae* and *Charopinus ramosus* with the cephalothorax bent forwards so that the present species is not to be excluded from the genus on that basis.

The closest resemblance to the present material, within the genus *Charopinus*, is shown by *Charopinus ramosus* as described and figured by T. and A. Scott (29, 30). This species has the cephalothorax projecting forwards and the mouth parts exhibit a great similarity to the specimens at hand. The main difference of the mouth parts lies in the shape of the first maxilliped, which has a long and slender second joint. The first maxilliped of *C. dalmanni* (30) has a shape identical to that of *C. cameroni*. The mandible of *C. ramosus* also differs from the new species in being obliquely truncate at the tip. The mouth parts of *C. cluthae* (30) are also similar but this species possesses a bulla.

The body shape and the proportions as well as the configuration of the second maxillae differentiate the known species of *Charopinus* from the present species.

The material is therefore assigned to the new species, *Charopinus cameroni*, in honor of Dr. T. W. M. Cameron.

Bere (2) in her description of *Lernaeopodina longimana* from *Raja scabrata* from the Bay of Fundy mentioned a strange specimen, differing from the others in possessing second maxillae without a bulla and with dichotomous ramefying branches. The first maxillae of this specimen were "tipped with three setae instead of two", like *C. cameroni*, but "the palp, instead of having a bifid appearance ended bluntly and bore three small spines". It is possible that this was a specimen of *Charopinus cameroni*.

Clavella uncinata (*Müller*)

Host: Gadus callarias

Habitat: Gills, buccal cavity, anal region

Abundance: These copepods are situated in more sheltered places and are more securely attached than *Caligus or Lepeoptheirus* and the number observed on each fish probably gives the true abundance of infection. The number cited refers to the female specimens. One or two males were usually found attached to each female.

June 24, 1947,	2 specimens from	1 fish
June 25, 1947,	13 specimens from	34 fish
July 3, 1947,	5 specimens from	10 fish
July 7, 1947,	18 specimens from	15 fish
July 11, 1947,	4 specimens from	70 fish
July 21, 1947,	42 specimens from	21 fish
Aug. 4, 1947,	14 specimens from	12 fish
Aug. 5, 1947,	2 specimens from	9 fish
Aug. 8, 1947,	28 specimens from	21 fish
Aug. 11, 1947,	4 specimens from	10 fish
Aug. 13, 1947,	9 specimens from	100 fish

Discussion

Wilson (39) and T. and A. Scott (29, 30) reported the species *Clavella uncinata* from the gills of gadoids and the present material seems to agree with their descriptions.

Leigh-Sharpe (14) in his revision of the British species of *Clavella* stated: "The members of the genus are pre-eminently parasitic on gadoid fishes, each species of *Gadus* is accompanied by a characteristic species of *Clavella*. Where

two or more species of the latter occur in the same host, each has a definite location, thus with

Gadus morrhua { *C. sciatherica* occurs in buccal cavity, pharynx. / *C. iadda* occurs on the skin, fin, tail, anus.

One of the most decisive characters serving for identification is the bulla. This varies according to the species, (*a*) in shape being spherical, ovate, clavate, or otherwise and (*b*) in respect to its channelings. In *C. iadda* each channel divides into four. In *C. sciatherica* the two channels unite to form a single channel, which afterwards forks, each branch dividing into four". He also reported that the bulla of the latter is spherical and that of the former ovate, and he gave drawings to illustrate these points. Leigh-Sharpe doubted the existence of the species *Clavella uncinata*.

In the present investigation, the material from the gills and buccal cavity was not kept separate from that of the anal region because it was not realized, at the time of collection, that there was a possibility of two species being present. But although numerous specimens were collected from the latter region, a thorough examination of each bulla revealed only one that could correspond to the description of *C. iadda*.

Furthermore, Bere (1) and especially Wilson (39) reported only the one species *Clavella uncinata* from North American cod, although they must have been aware of Leigh-Sharpe's previous publication.

The present material is therefore assigned to the species *Clavella uncinata*.

Acknowledgments

This investigation has been carried out with the aid of a Bursary from the National Research Council of Canada, under the direction of Prof. T. W. M. Cameron, Chairman of the Department of Parasitology, McGill University, Macdonald College, Que.

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THE DISTRIBUTION OF RADIOACTIVE ARSENIC IN THE ORGANS OF POISONED INSECT LARVAE[1]

By F. O. Morrison[2] and W. F. Oliver[3]

Abstract

Radioactive arsenic trioxide, containing As^{76} injected in solution into the haemolymph of last instar *Tenebrio molitor* L. larvae, distributed itself throughout the haemolymph, body wall, fore-, mid-, and hindgut, and Malpighian tubules within one hour and showed little change in distribution after as much as 20 hr. even though most larvae remained alive. When injected into the gut it showed little sign of escaping. Fifty instar *Phlegethontius quinoquemaculata* Haw. larvae fed the dry active arsenic trioxide absorbed only very small amounts. The largest portion remained in the gut if the specimen died or was eliminated within 20 hr. if the specimen lived. As little as 10^{-11} gm. arsenic was detectable in the digested insect organs. The use of a dipping counter on aliquots of the acid tissue digest provides a simple and accurate means of counting samples and is to be recommended in studies of this nature.

Introduction

It appears that the quantitative determination of radioactive insecticides in the individual organs of poisoned insects may prove a very delicate technique for following a toxin to the seat of activity and thus throw light on the fundamental action involved (1, 2, 3). With this in mind the authors undertook to investigate the possibilities of radioactive tracer work in the field of insect toxicology. Arsenic was chosen as the toxin because of its availability and nonvolatility.

Materials and Procedure

Arsenical Formulation

Active arsenic trioxide containing As^{76} was obtained from the National Research Council Laboratories at Chalk River. It was formed by As^{75} (n, γ) As^{76} reaction as indicated by the determined half-life of 26.77 hr. (Compare the value 26.8 hr. given in Seaborg's table (6).) The active insecticidal solution was prepared, on each occasion, as follows: 0.104 gm. of active arsenic trioxide (specific activity on arrival: 8 mc. per gm.) was added to 75 ml. of distilled water; 0.45 gm. of sodium carbonate and three drops of 40% sodium hydroxide solution were added to ensure solution of the arsenic trioxide; 1.981 gm. of sodium chloride was dissolved in this to render the solution approximately isotonic with the body fluids of the mealworm (5); and finally distilled water was added to make up to 104 ml.

Holder for Mealworm Larvae

A holder for mealworm larvae was constructed from two pieces of glass tubing of suitable bore, plugged at one end and held by pieces of rubber

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[2] *Associate Professor of Entomology.*

[3] *Associate Professor of Physics.*

stoppers, fitted into grooves in a firm base. This was mounted under a low power binocular microscope.

Injection Apparatus

A No. 22 hypodermic needle was attached to a tuberculin syringe clamped firmly to a retort stand and so adjusted that a slight movement allowed the needle to penetrate the firmly held specimen dorsolaterally through the intersegmental membrane between the second and third abdominal segments. A hand lens was used to read the graduations on the syringe.

Digestion Apparatus

Standard micro-Kjeldahl flasks and still smaller flasks blown from pyrex tubing were used for the digestion of the organs.

Counter and Auxiliary Equipment

A thin glass walled dipping counter (Distillation Products Incorporated) with a quenching circuit was used. Aliquots of the digest were placed in glass tubes with internal diameter 3 mm. greater than the diameter of the counter. These were placed beneath the counter and raised by a rack and pinion. Thus the same relative position of sample and counter was easily reproduced each time. Samples were counted for sufficient time to give no more than 2% error.

Test Animals

Last instar mealworm, *Tenebrio molitor* L., larvae (Coleoptera; Tenebrionidae) weighing an average of 0.2191 gm. each, reared on whole wheat flour, and last instar northern tobacco hornworm, *Phlegethontius quinquemaculata* Haw., larvae (Lepidoptera: Sphingidae) supplied by Mr. C. J. S. Fox, Entomologist in Charge, Dominion Entomological Laboratory, Chatham, Ont., were used as test animals.

Experimental Procedure

1. Fifteen last instar mealworm larvae were dissected and the organs pooled and weighed wet in weighing bottles. Approximately 20% of the live weight was lost by desiccation during dissection.

2. Last instar mealworm larvae were injected with 0.01 ml. of radioactive arsenic trioxide solution (0.00001 gm. arsenic trioxide) and were retained for varying intervals before dissection. Several similarly injected larvae were placed on Eastman X-ray films to secure radioautographs.

After the desired interval larvae were dissected and separated into foregut, midgut, hindgut, Malpighian tubules, body contents, and body wall. These portions were then digested in small amounts of hot nitric and sulphuric acid*

* *This is the method of digestion used when determining arsenic in organic matter by the Gutzeit or bromate methods. The condensed vapors from the digestion of insect tissues containing larger amounts of nonradioactive arsenic trioxide showed no trace of arsenic by the former test.*

until the solution was clear. While the activity varied from 0.08 μc. to 0.003 μc. per injection it was possible to work with one larva at a time, but later the parts of from 2 to 10 larvae were grouped for digestion.

Attempts to precipitate the arsenic from the digest, filter it off, and count the activity of the dry precipitate proved subject to errors that made the reproduction of results very difficult. In the work reported here a dipping counter was used, the acid digest being diluted to 25 ml. at room temperature, and two aliquots of 4 ml. each pipetted out and "counted".

3. Last instar northern tobacco hornworm larvae were fed unmeasured amounts of the dry active arsenic trioxide by "buttering" it onto a tomato leaf. No difficulty was experienced in getting the larvae to consume the treated leaf area. These larvae were then kept on tomato leaves and later dissected. Digests of organs, faecal pellets, and regurgitated material were "counted" for radioactivity.

Results

1. Table I gives the results of mealworm larvae injection in terms of the percentage of total activity (arsenic) in each organ; Table II gives the same information per unit weight of organ. The latter values were determined by

TABLE I

PERCENTAGE* OF TOTAL ARSENIC FOUND IN ORGANS OF LAST INSTAR *Tenebrio molitor* LARVAE DISSECTED AT VARYING INTERVALS AFTER 0.00001 GM. OF As_2O_3 HAD BEEN INJECTED INTO THE HAEMOLYMPH OF EACH LARVA**

Interval in hours (injection to dissection)	Number of larvae	Body wall	Body contents	Malpighian tubules	Foregut	Midgut	Hindgut
1	4	67	15	3	3	10	2
1.5	8	67	17	6		6	4
2.5	4	66	19	3	1	9	2
4	5	65	17	5	2	8	3
7	4	70	13	6	2	6	3
10	10	64	21	6	1	5	3
16	5	61	25	4	1	7	2
20	4	58	25	7	1	7	2

* *Expressed in terms of percentage of the sum of the amounts found in the organs.*

** *All counts have been corrected for background, counter variability, and decay, the last having been determined by actual counts on aliquots of a standard solution of known dilution of the arsenic trioxide.*

using the average wet weights of organs dissected from 15 last instar mealworm larvae. The weights were: body wall, 0.931 gm.; body contents, 0.0419 gm.; Malpighian tubules, 0.0034 gm.; foregut, 0.0013 gm.; and hindgut, 0.0029 gm. These figures total approximately 20% less than the average live weight of the 15 worms, the loss being accounted for by desiccation during the dissection operation. The loss is probably not uniform for all tissues as the liquid tissues

TABLE II

ARSENIC DISTRIBUTION IN ORGANS OF LAST INSTAR *Tenebrio molitor* LARVAE DISSECTED AT VARYING INTERVALS AFTER 0.00001 GM. OF As_2O_3 HAD BEEN INJECTED INTO THE HAEMOLYMPH OF EACH LARVA: EXPRESSED AS PERCENTAGE OF ARSENIC PER UNIT WET WEIGHT OF ORGAN

Interval in hours (injection to dissection)	Number of larvae	Body wall	Body contents	Malpighian tubules	Foregut	Midgut	Hindgut
1	4	13	7	14	33	17	11
1.5	8	16	9	36		12	27
2.5	4	17	11	18	15	19	19
4	5	13	8	27	23	7	22
7	4	13	5	33	24	9	16
10	10	15	11	18	23	10	23
16	5	14	13	22	23	14	14
20	4	13	12	43	10	12	10

would be expected to suffer the greater loss and it therefore seems questionable whether the weights given above should be corrected for this loss or not before being used to determine the toxin per unit weight. No correction was made.

2. Radioautographs of injected mealworm larvae gave either diffuse pictures of the entire body resulting from haemolymph injection, or a faint line indicating the position of the gut when the arsenic had been delivered into the alimentary canal by the injection needle. Since reproductions from such pictures lack detail they are not included here. (Cf. Norton and Hansberry (4).)

3. A fifth instar hornworm larva fed an unmeasured quantity of active arsenic was dissected after two hours: faecal pellets passed at one hour after feeding showed 0.1% of the total activity; those passed after two hours, 9.1%; the body wall, 13.1%; and the Malpighian tubules, 0.8%; while the gut and body contents showed 77.2%. As the gut was punctured during dissection the activities of the gut and body contents were grouped together. Some slight contamination of the body wall may have resulted from the puncture.

A second hornworm larva dissected 19 hr. after being fed was still alive and had to be anaesthetized prior to dissection. The arsenic distribution was: faecal pellets, 90.0%; body wall, 3.1%; Malpighian tubules, 0.7%; body contents, 1.6%; and gut, 4.0%.

A third hornworm larva dissected 24 hr. after feeding, but dead for some time, showed: faecal pellets, 0.2%; regurgitated material, 12.1%; body wall, 7.8%; Malpighian tubules, 0.4%; body contents, 2.0%; and gut, 69.4%.

Discussion

It would appear that arsenic trioxide injected into the haemolymph of mealworm larvae is by the end of one hour distributed through all the organs

and little change occurs after that, even though the larvae remain alive (though somewhat inactivated) for many hours. What appeared to be a trend of adsorption from haemolymph to organs in earlier tests made on larvae held back from pupation by refrigeration at 34° F. was not borne out in the later tests on nonrefrigerated larvae reported here. This difference might have been due to physiological inactivation. Expressed as percentage of arsenic per unit weight of organ the distribution was nearly uniform in all organs measured. Curiously enough the body contents, including the haemolymph into which the injection had been made, gave the lowest activity reading per unit weight in spite of the fact that the largest part of the weight loss during dissection was likely to have taken place from this liquid tissue.

The results demonstrate clearly the high sensitivity of the technique. Even after the activity had dropped to less than 1/1000 of the original, less than 1% of the total injected into a larva was measurable; in other words, detection of quantities of the order of 10^{-11} gm. was possible.

Attempts to hold back the development of tobacco hornworm larvae, so that they would be available as and when desired, failed. The size and readiness with which these test animals ingest dry material, however, makes them very desirable. Then too, their larger size makes possible the use of dosages detectable even after the activity of the material has fallen off greatly. The indication that ingested arsenic trioxide was largely retained in the gut of these animals and rapidly eliminated in the faecal matter of those that survive is what might be expected from the insolubility of arsenic in this form.

Acknowledgments

In this first published paper on results obtained in this laboratory using the tracer technique in agricultural problems it is the desire of the authors and of the Macdonald College Tracer Committee to thank the National Research Council for the financial aid that made an equipped laboratory possible and assisted in getting various projects of this nature under way.

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SOME EFFECTS OF TEMPERATURE AND OXYGEN PRESSURE ON THE METABOLISM AND ACTIVITY OF THE SPECKLED TROUT, *SALVELINUS FONTINALIS*[1]

By J. M. Graham[2]

Abstract

Two levels of oxygen uptake were measured at temperatures from 5° C. to 24° C. on yearling speckled trout having a mean weight of 27 gm. These levels were the minimum resting rate in the diurnal cycle (standard rate) and the rate when induced to activity in a rotating chamber (active rate). The trout were thermally acclimated to the temperatures at which the experiments were performed. The standard rate of oxygen uptake increased with increasing temperatures up to the ultimate upper lethal temperature (25.3° C.). The active rate of oxygen uptake increased with increasing temperatures up to approximately 19° C. Above this temperature it fell again. The consequence of this difference in the response of the standard and active rates of oxygen rate to temperature is that the difference between these two levels increases rapidly up to a temperature of 16° C. and falls again thereafter. This is interpreted as indicating that the optimum temperature for the activity of the speckled trout is in the neighborhood of 16° C. The activity of speckled trout in relation to temperature was measured in terms of the maximum speed that they can maintain indefinitely. This speed was also found to be a maximum at a temperature of 16° to 20° C., at which region occurs the greatest difference between the standard and active rates of oxygen uptake.

The oxygen uptake of active speckled trout was measured over decreasing partial pressures of oxygen, and was found to become dependent on the oxygen pressure below a certain critical level. These critical pressures change with temperature from 100 mm. Hg at 5° C. to 150 mm. Hg at 24.5° C. Water containing less than 75% air saturation of oxygen reduces the activity of speckled trout at all temperatures. Above 20° C. fully saturated water is required to allow full scope to the activity of speckled trout. The minimum oxygen requirements for existence of the speckled trout at the standard metabolic level are estimated to vary from 30 mm. Hg at 5° C. to 79 mm. Hg at 24.5° C. It must be emphasized, however, that these values are conservative. The lethal levels of oxygen were measured for speckled trout and found to rise from 19 mm. Hg at 3.5° C. to 45 mm. Hg at 23° C.

Introduction

The speckled trout, *Salvelinus fontinalis* (Mitchill), is characteristically an inhabitant of cool well-aerated waters. Speckled trout have been found to frequent waters varying in mean summer temperature from 10.5° C. (8) to 21° C. (7). Minimal safe oxygen concentrations for speckled trout have been set by field workers at 4 to 5 p.p.m. (7, 9, 12, 26).

The temperature relations of speckled trout have been studied in further detail in the laboratory. Brett (3, 4) and Fry, Hart, and Walker (17) established the upper lethal level of temperature for the species. Rogers (28) described the relation of temperature to cruising speed of speckled trout. Their preferred temperature has been investigated by Fisher and Elson (13) and again by Elson (11) in connection with its relation to the temperature at which the fish respond maximally to an electrical stimulus.

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Contribution from Ontario Fisheries Research Laboratory, Department of Zoology, University of Toronto, Toronto, Ont.

[2] *Graduate Student.*

The purpose of the present work is to supplement the investigations listed so as to permit the definition of the scope for continuous activity that various combinations of oxygen pressure and temperature may present to the speckled trout. The method of attack was that used by Fry and Hart (16) for the goldfish. It included essentially the measurement of the standard and active levels of metabolism over a range of temperatures and oxygen pressures, and the determination of maximum steady activity at the various temperatures. To delimit further the environment suitable for speckled trout the lower lethal levels of oxygen were estimated from the metabolic data and also determined by direct experimentation.

Materials and Methods

The speckled trout used in all these experiments were yearlings obtained from provincial hatcheries. Their weights ranged from 17 to 65 gm. with a mean of 27 gm. Liver was fed to the fish every two days, the feeding times being arranged so that at least 24 hr. elapsed between them and the time the fish were used in experiments. In all cases the fish were maintained at the temperature at which the experiment was to be carried out for a period of some days or weeks prior to the experiment.

The standard metabolism of the trout as described here is the minimum metabolic level found in the 24 hr. cycle. It is considered an approximation of the basal level. As is commonly the procedure, the standard metabolism was measured by recording the oxygen intake of the resting fish. The method used is described by Fry and Hart (16). Each fish was enclosed in a 2 l. flask through which flowed water of constant temperature. This flow was stopped over certain periods and the oxygen intake estimated by taking the difference between the oxygen content of the water in the flask before and after the stoppage. To accommodate the rise in metabolic rate with temperature, the duration of the period during which circulation through the flask was cut off was decreased from three hours at 5° C. to one hour at 10° C. and over. Water was allowed to flush through the flasks for at least an hour between each test period.

Keys (22), Wells (29), and Black, Fry, and Scott (2), among others, have recorded that handling of fish raises their oxygen consumption well above the resting level, and that the excited condition may last for some time after the fish is not visibly active. For this reason the speckled trout were left undisturbed in the flasks at least 24 hr. before any water samples were taken. The fish were fed liver an hour or so before being placed in the flasks so that a fairly standard nutritional state was obtained.

The active respiratory rates were obtained by measuring the oxygen intake of fish swimming at a maximum steady rate in opposition to the motion of water in a rotating chamber. The chamber and the details of the method of following the oxygen intake of active fish are described by Fry and Hart (16). In these experiments the usual procedure was to place two trout in a

measured amount of water (3 or 4 l.) and to withdraw water samples for oxygen analysis every 10 to 20 min. Since periodic tests for nitrite in the water proved negative, the unmodified Winkler technique for the measurement of dissolved oxygen was used in determining both active and standard metabolic rates.

During the measurement of the active rate, the rotation was held at a speed that kept the fish as active as possible; no particular record was kept of the swimming rates, however. To test whether or not this course of action was justified, the oxygen intake was measured of one fish, first as the chamber remained still and then as it rotated at 27 r.p.m. Fig. 1 illustrates the fall of

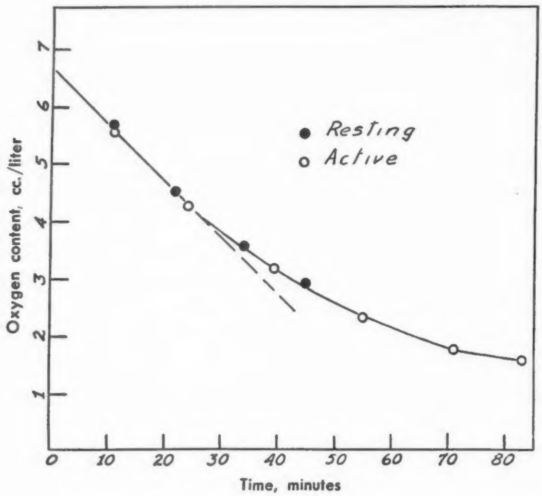

FIG. 1. *The extraction of oxygen from water in the annular chamber by a 62.3 gm. speckled trout acclimated to 14.5° C.*
Resting: the chamber at rest.
Active: the chamber rotating at 27 r.p.m.
The measurements at rest were taken first.

oxygen in the chamber as the fish extracted it over a period of time. Somewhat surprisingly, there is no difference in rate of oxygen intake within the two experimental conditions. The handling of the fish as it was first put into the chamber was evidently sufficient stimulus to activity and eliminated the necessity of further agitating during the next half hour or so. In this respect the trout behaves much as the perch, sunfish, and bullhead whose excitabilities have been similarly tested (2).

From the initial straight part of such curves as shown in Fig. 1, the maximum active respiratory rate was calculated. The amount of carbon dioxide that accumulated during these measurements of active metabolism does not appear to have significantly affected the rate of oxygen uptake. In 21

experiments, marble chips, which kept the carbon dioxide pressure to 4 mm. Hg and less, were placed in the bottom of the chamber. These experiments gave essentially the same result as when no chips were used. Without chips, carbon dioxide pressures of the order of 9 mm. were attained at the end of the longer runs.

Both the standard and active rates of oxygen uptake per unit weight were found to decrease with size, but the precise relationship has not been determined in the present instance. It must be realized, therefore, that the rates presented here, although reduced to rates per unit weight, hold good only for trout 20 to 65 gm. in weight.

Direct measurements of the lethal level of oxygen at four temperatures were made by subjecting the fish to running water in which the oxygen content had been reduced. The apparatus first used to measure lethal levels of oxygen consisted of five 2 l. Erlenmeyer flasks connected in series by rubber and glass tubing. Water of regulated temperature flowed through the series. As the water passed through successive flasks the fish therein lowered the oxygen content in such a way that a decreasing gradient of oxygen was set up between the first and last flasks. To remove the free carbon dioxide, the water flowed through a tube containing crushed marble as it passed from each flask to the next. The experiment recorded at 3.5° C. was done in this apparatus. It was found, however, that the oxygen content of the flasks fluctuated with the time of day. Apparently the greater level of external stimuli in the daytime (or an endogenous activity cycle) prompted the fish to increase their metabolic rates even though oxygen was withheld. For this reason the apparatus was discarded in favor of another, which included a fractionating column made of 1 liter flasks described elsewhere (15). Water introduced into the top of the column met nitrogen rising from an inlet at the bottom. As the water descended its oxygen content became progressively lowered so that it was possible to draw off water of a different constant oxygen level from each of the five flasks constituting the column. The oxygen content of the whole series could be raised or lowered by introducing the water at different distances up a four foot glass tube at the top of the column. For that purpose, four inlets were fused up the tube about 10 in. apart.

Five levels of oxygen lying about 0.5 cc. per liter apart could be obtained by use of this apparatus. Such a gradient was suitable to establish roughly the whereabouts of the lethal level. For a more exact determination, some of the flasks were replaced by test tubes fitted together and provided with outlets in the same manner as the flasks. There was a difference of about 0.1 cc. per liter of oxygen in water drawn from successive test tubes. To keep the gradient steady, especially when water above 15° C. was used, the temperature had to be maintained within 0.3° of the test temperature.

The trout were placed in Erlenmeyer flasks submerged in a constant temperature bath supplied by water from the Erlenmeyer overflows. To allow time for them to settle, the fish were fed and put into the flasks at least 12 hr. before the experiment was begun. During this preliminary period the

Erlenmeyers were flushed through with aerated water. At the same time the nitrogen was turned on in the equilibrator column so that the gradient was established and steady when needed. To start the experiment the rubber tubing supplying aerated water to the inlet of each Erlenmeyer was replaced by tubing from the outlets of the gradient column. In this way the oxygen levels in the Erlenmeyers could be changed without disturbing the fish. Each experiment was carried out over a minimum period of 24 hr.

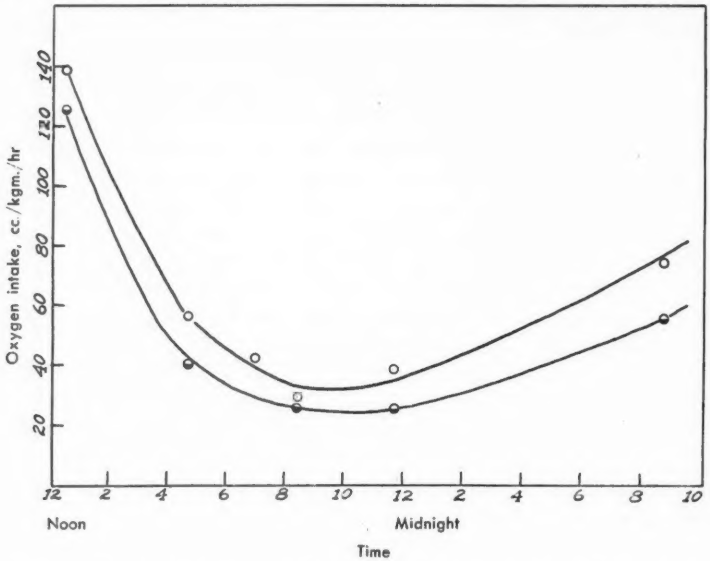

FIG. 2. *The relation of oxygen intake to time of day in two resting speckled trout acclimated to 5° C. Data of A. H. Lawrie (unpublished).*

Results

(a) The Effect of Temperature on the Standard Metabolic Rate

Although the room in which the standard metabolism experiments were done was kept reasonably quiet, and light was at a minimum, a diurnal fluctuation in the metabolic rate of the "resting" fish persisted. This behavior is common to many species of both fish and mammals (31) and was to be expected in the trout. An example of such a change of rate with time of day is displayed in Fig. 2, which is a plot of data obtained using trout acclimated to 5° C. Though the relation of this fluctuation to time of day would indicate a simple response to light intensities, there have been other experiments done with speckled trout (19) and mammals (21) in which it was found that the fluctuation persisted for some time even in continued darkness.

The lowest activity occurred at approximately 12 p.m. in experiments done over 24-hr. periods at 5°, 10°, and 15° C. Consequently, the respiratory rates

were measured only at night for the last three acclimation temperatures, starting at 11 p.m. and concluding at 7 a.m. The lowest point on each plot of respiratory rate against time of night was taken as the standard metabolic rate.

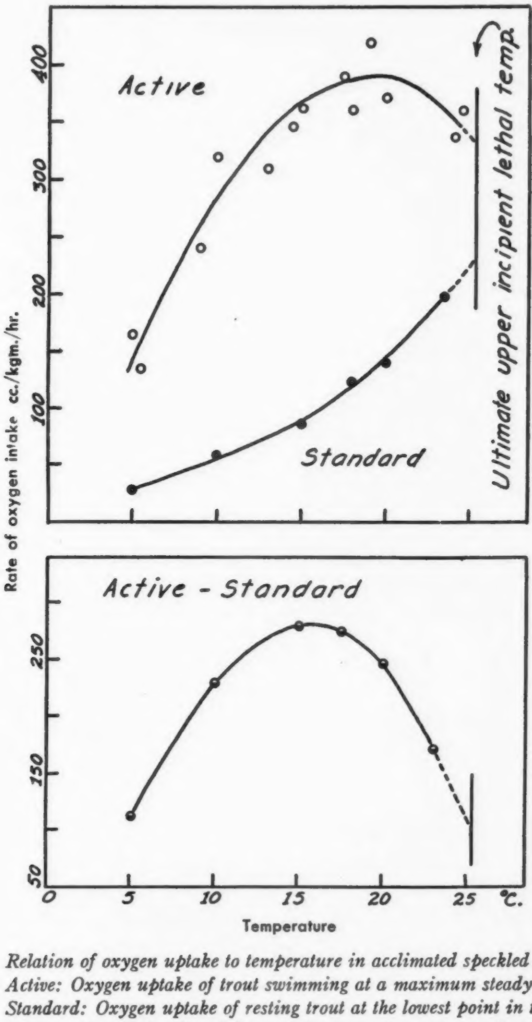

FIG. 3. *Relation of oxygen uptake to temperature in acclimated speckled trout.*
Active: Oxygen uptake of trout swimming at a maximum steady speed.
Standard: Oxygen uptake of resting trout at the lowest point in the diurnal cycle.
Active – Standard: The difference between the active and standard levels of oxygen uptake at the various acclimation temperatures.

The resting respiratory rates of three fish were measured at each acclimation temperature. At 18° C. and 20° C. it was necessary to discard data obtained from one of the three fish in each case for it was obvious from the results

that these fish had remained active all night. In this connection, it will be noticed that at the peak of the diurnal cycle of the fish acclimated to 5° C. (Fig. 2) the metabolic rate of the spontaneously active fish is about the same (140 cc. per kgm. per hr.) as that of the fish stimulated to activity at 5° C. (cf. the "active" curve, Fig. 3).

The standard rates at the various acclimation temperatures are listed in Table I and plotted in Fig. 3. There is a continuing increase of standard metabolism with increasing temperature right up to the lethal level.

TABLE I

STANDARD METABOLIC RATES OF SPECKLED TROUT AT DIFFERENT LEVELS OF THERMAL ACCLIMATION

Acclimation temperature, ° C.	Weights of trout, gm.	Oxygen intake, cc./kgm./hr.	
5	17.6 22.5 25.4	39.6 25.3 17.7	Av. 27.5
10	13.3 19.1 20.4	54.0 78.4 43.7	Av. 58.7
15	16.4 21.4 26.9	91.2 98.6 64.7	Av. 85.2
18	29.7 34.5	114 132	Av. 123
20	17.9 28.6	152 128	Av. 140
23.5	20.1 29.2 29.5	199 204 190	Av. 198

Note: The standard metabolic rates at 5° C., 10° C., and 15° C. were provided by Mr. A. H. Lawrie from unpublished data.

(b) The Effect of Temperature on the Active Metabolic Rate

The maximum steady respiratory rates found for the speckled trout at oxygen pressures of 160 mm. and greater have been plotted against temperature in Fig. 3 and are listed in Table II. The rate rises rapidly with temperature, reaching a peak at about 19° C., after which it falls quite sharply. The experiments were taken to within half a degree Centigrade of the ultimate upper incipient lethal temperature found for this species, 25.3° C. (17).

(c) The Effect of Oxygen Pressure on the Rate of Oxygen Uptake at Different Temperatures

The method used for determining the active metabolic rate has the advantage that it permits a measure of respiration at decreasing oxygen

TABLE II

ACTIVE METABOLIC RATES OF THERMALLY ACCLIMATED SPECKLED TROUT IN THE INDEPENDENT RANGE OF OXYGEN PRESSURES IN RELATION TO TEMPERATURE

Acclimation temperature, ° C.	No. of trout used in one determination	Weights of trout, gm.	Oxygen intake, cc./kgm./hr.
5	2	33.3 38.2	165
5.5	3	17.6 24.6 21.4	135
9	2	35.5 31.7	241
10	3	15.6 19.0 20.1	320
13	3	17.9 19.1 15.0	350
13	2	36.8 43.2	287
14.5	1	62.3	347
17.5	2	32.8 27.6	390
18	2	74.7 27.8	361
19	2	28.7 21.3	424
20	3	22.0 23.9 18.8	371
24	3	22.5 33.3 23.8	337
24.5	3	34.4 40.3 40.7	361

concentrations. Fig. 1 is a typical plot showing the decrease of oxygen in the chamber with time. There is an initial linear phase in which the rate is independent of the level of oxygen. Following this linear phase, which is terminated in Fig. 1 at approximately 20 min., is a phase in which the rate falls in proportion to further decrease in oxygen pressure. Time can be eliminated from this diagram if tangents are drawn to the curve and the rate of oxygen uptake per unit time determined from them. These rates can be plotted against the appropriate oxygen pressure. Such rate curves are presented in Figs. 4 and 5 for the different temperatures at which the active metabolism was measured.

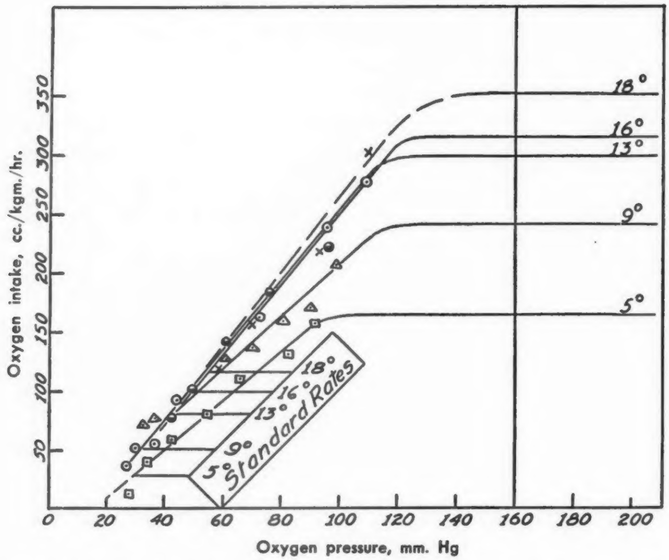

FIG. 4. *Relation of maximum steady rate and standard rate of oxygen intake to oxygen pressure at various acclimation temperatures. For the significance of the standard rates – see the text, page 285.*

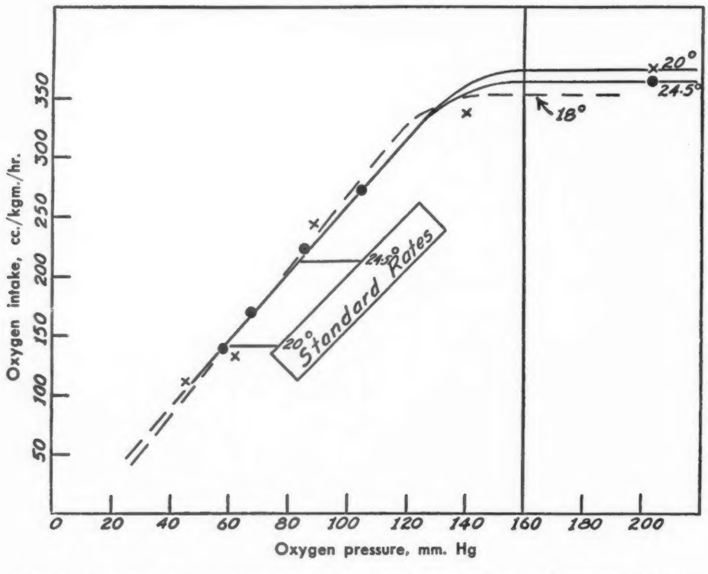

FIG. 5. *Relation of maximum steady rate and standard rate of oxygen intake to oxygen pressure at various acclimation temperatures.*

Fig. 4 shows the results of experiments at temperatures up to 18° C., Fig. 5 those at 20° C. and 24.5° C. At each temperature, the active rate of oxygen uptake remains constant down to a certain oxygen pressure. Below this pressure, the rate decreases with further decrease in the partial pressure of oxygen along a course that is approximately linear as far as the experiments were taken. In the range of oxygen pressures where the rate of respiration was dependent on the oxygen pressure, the trout at 9° C. could take up oxygen faster than could the trout at 5° C. The trout at 13° C. had a still further advantage in this respect, but at higher temperatures there did not appear to be any further increase in the rate at which oxygen could be taken up at a particular oxygen pressure in the region of respiratory dependence, as the overlapping of the curves for 13° C., 16° C., 18° C., 20° C., and 24.5° C. indicates. The pressure at which the active respiration passes from the independent to the dependent phase appears to increase with temperature throughout the biokinetic range.

(d) Lethal Oxygen Levels in Relation to Temperature

The experimental results are illustrated in Fig. 6, except for the experiment at 3° C., the survival time of each individual being represented by a point. Since the relationship in Fig. 6 between lethal oxygen level and time to death

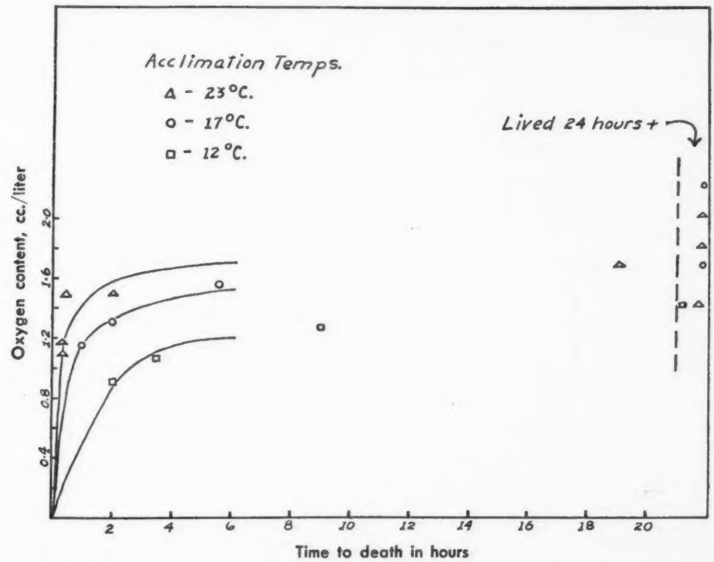

FIG. 6. *Survival times of speckled trout exposed to various low levels of oxygen.*

appeared hyperbolic, the tolerance levels were estimated by replotting the data, using the reciprocals of the survival times, and fitting a straight line to the points by eye. The tolerance levels were then estimated by extrapolating

these lines back to $1/t = 0$. The tolerance levels thus estimated are given in Table III and are illustrated in Fig. 10. The lethal level changes considerably with temperature, being estimated at under 20 mm. Hg at 4° C. but rising to about 50 mm. at 22° C.

TABLE III

RELATION OF ACCLIMATION TEMPERATURE TO MINIMUM OXYGEN REQUIREMENTS OF SPECKLED TROUT

Temperature, ° C.	Estimated oxygen pressure allowing no excess activity, mm. Hg	Measured lethal level of oxygen pressure, mm. Hg
3.5	—	19
5	30	—
9	32	—
12	—	27
13	43	—
16	50	—
17	—	38
18	54	—
20	59	—
23	—	45
24.5	79	—

Discussion

(a) The Effect of Temperature on the Active and Standard Metabolic Rates and their Relation to Activity

As might be expected, the relation between standard metabolism and temperature showed no departure from the characteristics for this relationship found in other species of fish. The proportional rate of increase drops gradually with increasing temperature but the absolute rate increases throughout the range. A comparison of the proportional rates of change with those of the goldfish (16) shows no substantial difference in temperature coefficients. This observation is contrary to the suggestion of Fry (14) that the slope would be less in the case of a fish adapted for activity at low temperatures.

As is shown in Fig. 3, the course of the relationship of the active oxygen uptake differs substantially from that of the standard rate. In particular, the active rate drops with increasing temperature at temperatures above 20° C. This behavior is similar to that found for the goldfish (16) but is not universal for all fishes as the data of Paul and Fry for the bullhead (14) and unpublished data of the author for the rainbow trout and brown trout indicate. The cause for this drop in the active metabolic rate at temperatures still well below the ultimate incipient lethal is unknown. However, it is tentatively concluded that it is due to some limit being reached in the capacity of the accessory systems of the organism responsible for the marshalling of the metabolites. The course of the relation of active metabolism to temperature

pehaps explains the surprising results of Montuori (25), which have never been satisfactorily explained. Montuori found in the case of three species of fish that there was no change in the rate of respiration when fish were transferred from 20° C. to 30° C. His technique was such that undoubtedly his measurements were taken when his subjects were in an excited state. Thus, it is quite possible that, in the species that he was investigating, the levels of the active rate at 20° C. and at 30° C. could have been the same, the point at the lower temperature being on the ascending limb and that at the upper temperature on the descending limb of the curves.

The active and standard metabolic rates were established primarily with a view to providing an explanation for the relation of activity of the fish to temperature such as was pointed out by Fry and Hart (16). It is presumed that the metabolism available to provide energy for external work is the difference between the active and the standard levels, neglecting the facts that the standard is not the true basal and that the active includes also the extra cost of maintaining activity. Therefore the difference between the active and standard metabolism has also been plotted in Fig. 3. This curve shows a pronounced rise and fall with a peak at approximately 16° C.

The validity of the conclusion that the scope for activity is given by the difference between the active and standard curves of oxygen uptake is supported by observations on the relation between temperature and the cruising speed of speckled trout. The cruising speed has been taken as the maximum steady speed that the fish is able to maintain indefinitely. These measurements have been made in two ways. The original apparatus used by Rogers (28) was a trough in which a current of water was generated by means of a propeller. The cruising speeds have again been measured in the same rotating chamber that was used for the determination of the active metabolism. The details of this method have been outlined by Fry and Hart (16).

Fig. 7 is a plot of temperature against cruising speed of speckled trout as measured by Rogers (28) and by the author. With respect to the curve of the latter, the data illustrated by open circles were obtained in January 1948 and those by closed circles in July 1948. Though there is some discrepancy in the temperatures at which the greatest activity occurs in the two curves drawn, they both indicate an increase of activity with temperature to between 16° and 20° C. followed by a decrease at the higher temperatures. Below the cruising speed curves the differences between standard and active oxygen intakes has been plotted at corresponding temperatures. The general similarity in shape and in the relation of slope to temperature in the two curves suggests an explanation for the change of activity with temperature illustrated. Actually, the cruising speed is more directly related to the square root of the difference between active and standard respiratory rates. This relationship has been fully discussed in connection with the goldfish by Fry (14). Such a correlation between activity and oxygen intake has been similarly worked out by Hill *et al.* (18) for man and by Chadwick and Gilmour (5) for ***Drosophila.***

Hill subtracted the resting oxygen intake of the subject from the oxygen consumption as he walked and ran at various speeds and obtained a straight line relationship between this difference and a power of the speed. Chadwick and Gilmour obtained an increase of oxygen intake over the resting rate that varied directly with the square of the wing rate of *Drosophila*.

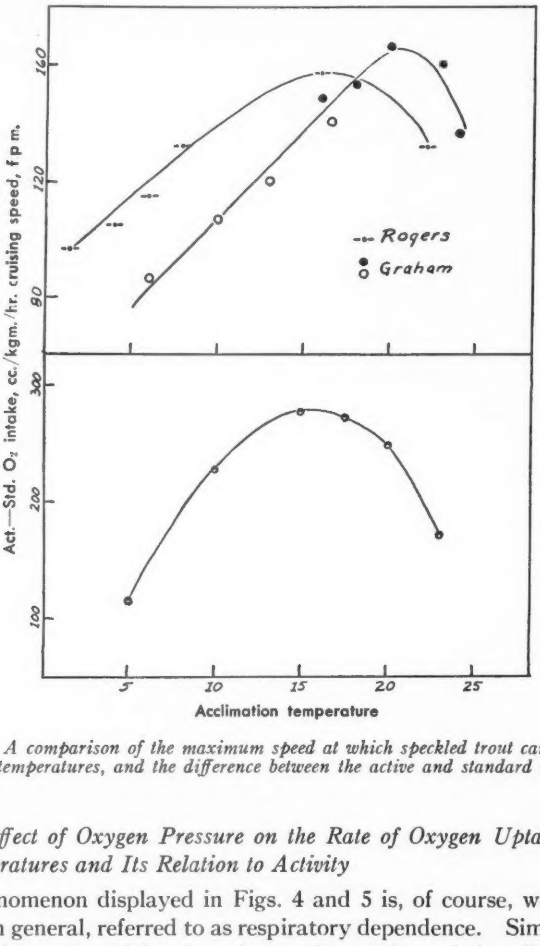

FIG. 7. *A comparison of the maximum speed at which speckled trout can swim steadily at various temperatures, and the difference between the active and standard levels of oxygen intake.*

(b) The Effect of Oxygen Pressure on the Rate of Oxygen Uptake at Different Temperatures and Its Relation to Activity

The phenomenon displayed in Figs. 4 and 5 is, of course, well known and has been, in general, referred to as respiratory dependence. Similar data have been recently presented for the salmon, the roach, and the pike by Lindroth (24) and more completely for the goldfish by Fry and Hart (16). There are numerous earlier but fragmentary examples.

The interpretation suggested for the nature and order of the curves is as follows. During the dependent phase, some rate in the process of uptake and transport of oxygen to the site of respiration is being limited by the oxygen

supply. At the temperatures of 5° C. to 9° C. and 13° C. the rate of supply at any given pressure in the dependent range is presumably improved by an increase in pumping rate of the ventilatory apparatus. At higher temperatures, apparently, the trout has not this advantage perhaps because of the high cost of respiration when water is the respiratory medium.

It is noteworthy that the oxygen uptake – oxygen pressure curves do not pass through the origin. The uptake approaches zero at an oxygen pressure of about 20 mm. Hg. Lindroth (23) noted a similar circumstance. He suggested that the pressure of oxygen at which the uptake fell virtually to zero corresponded to the unloading tension of arterial blood. This does not appear to be the whole explanation in the case of the speckled trout since 20 mm. Hg of oxygen should be sufficient to saturate the blood of speckled trout at the highest temperature investigated (20). Undoubtedly therefore the dynamics of the situation also enter into the case. The original oxygen content of water presented to the respiratory surface (20 mm. Hg) must be soon taken up by the blood in the lamellae and the pressure so quickly reduced that equilibrium is established at a pressure much lower than 20 mm.

At levels of oxygen where the active metabolic rate is reduced there must be some limiting of overall activity. An experiment to illustrate this effect in the case of the speckled trout is shown in Fig. 8. In this experiment the

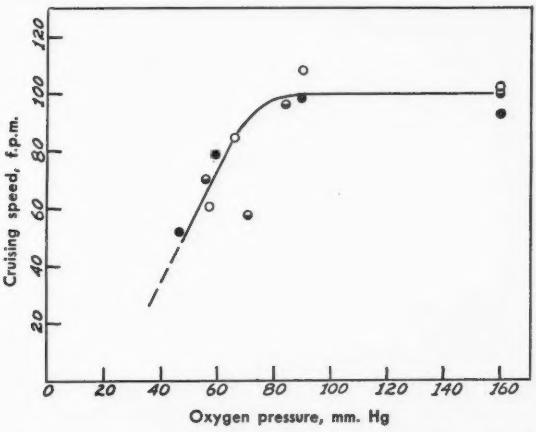

FIG. 8. *The maximum steady speeds that a speckled trout acclimated to 8° C. can maintain at that temperature in water containing various partial pressures of oxygen.*

oxygen pressure of the water in the rotating chamber was adjusted to various levels by bubbling various nitrogen – oxygen mixtures through it. The cruising speeds of three individual speckled trout were measured at each of these various levels of oxygen pressure with the results indicated in the figure. At oxygen pressures below 80 mm. Hg there is a steep falling off of the cruising speed. The agreement between this experiment and the relation between the

rate of oxygen uptake and oxygen pressure is only approximate. At the temperature in question (8° C.) the respiration would have been expected to become dependent upon oxygen pressure at 100 mm. Hg. However, the relatively short duration of the experiments makes it probable that the cruising speeds obtained at the lower pressures were in excess of those that would represent a true steady state.

The general order of reduction of activity consequent on reduction of oxygen pressure below air saturation is illustrated in Fig. 9. This figure

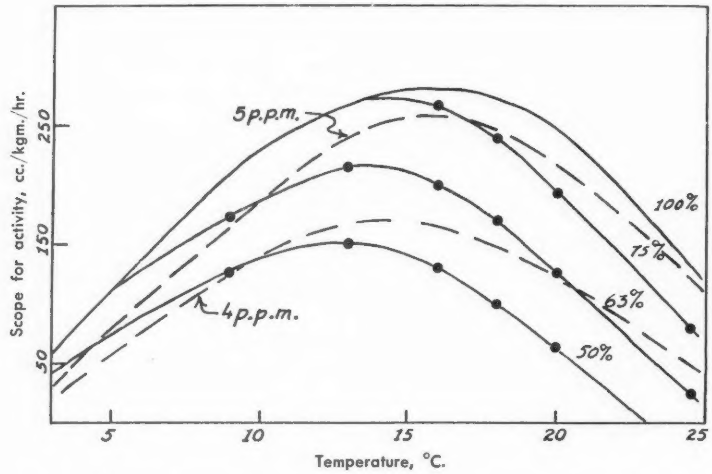

FIG. 9. *Relation between temperature and the scope for activity of speckled trout in waters of different percentages of air saturation. The two broken lines indicate the scope at 4 and 5 p.p.m., the range of oxygen that field workers have indicated as being the safe minimum for speckled trout.*

depicts the degree to which the active metabolism in a steady state could rise above the standard requirements. The profiles given have been expressed in per cent air saturation rather than mm. Hg pressures since the former terminology has been almost universal in fisheries biology.

From the point of view of providing sufficient oxygen to allow the speckled trout its full scope for activity it would seem from Fig. 9 that less than 75% air saturation would be detrimental to speckled trout at any temperature. Above 20° C. even reduction to 75% would be serious. This is in strong contrast to the requirements of such a fish as the goldfish in which reductions down to 25% air saturation have no effect. Two other levels of saturation, 63% and 50%, are shown in Fig. 9. The 63% line indicates that even at the ultimate lethal temperature death might not be due to oxygen lack. This value is in agreement with Brett (3) who found by experiment that an oxygen content down to 62% air saturation in the waters of his lethal baths did not affect the rate of dying. The 50% saturation level affects the scope

for activity over the whole biokinetic range of the speckled trout and would bring death by anoxia at a temperature somewhere between 20° C. and 25° C.

These laboratory findings are thus in close accord with the empirical level of 4 to 5 p.p.m. taken from field observations at summer temperatures. Five parts per million represent respectively 62, 70, 80, and 85% air saturation at temperatures of 10°, 15°, 20°, and 25° C. Thus this level represents almost exactly the safe minimum suggested by the experimental data. Four parts per million (50% air sat. at 10° C., 60% sat. at 20° C.) would appear to be definitely below the minimum for full activity.

(c) Lethal Oxygen Levels in Relation to Temperature

It has been proposed by Lindroth (23) and Fry (14) that the oxygen level at which the rate of oxygen uptake is reduced to no more than the requirements for standard metabolism can be taken as the minimum requirement for the existence of the organism. The standard levels of metabolism have been indicated on Figs. 4 and 5 by short horizontal lines. According to the above reasoning, the minimum oxygen levels for existence of speckled trout would be described by the oxygen pressure at which these horizontal lines cut the appropriate oxygen uptake – oxygen pressure curves. Thus in Fig. 4 at 5° C. the level of standard metabolism is that which occurs on the active oxygen uptake curve at 30 mm. Hg. This point was termed by Fry (14) as the "level of no excess activity". The levels of no excess activity are given in Table III for the various temperatures investigated and are illustrated in Fig. 10.

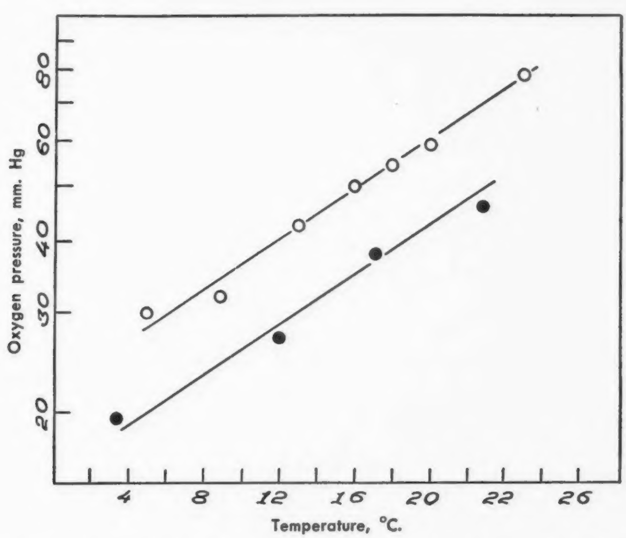

FIG. 10. *The relation of the level of no excess activity (open circles) and the lethal level of oxygen (solid dots) to temperature.*

The level of no excess activity changes considerably with temperature. At 4° C. it is approximately 26 mm. Hg while at 22° C. it is about 70 mm. Hg. Thus at 22° C., if the index is appropriate, the speckled trout requires water that is approximately 40% air saturated in order to exist without undertaking any appreciable amount of external work.

The experiments to measure the lower lethal levels of oxygen were carried out in order to test the validity of the estimates of the levels of no excess activity as measures of the lower levels of tolerance for oxygen. The level of no excess activity might give an erroneous value for one of two reasons. The estimate might be far too high because the standard rate of metabolism measured might include far too much expenditure for the maintenance of chance movements, or it might be unduly low because the standard rate was measured under conditions of high oxygen and the cost of ventilation would thus be at a minimum. When the oxygen level was reduced to the neighborhood of the level of no excess activity much more water would have to be pumped over the gills to supply the oxygen required to maintain the standard metabolic rate and the work thus involved might considerably increase the basal requirements of the animal.

The direct estimates of the lethal oxygen levels are compared with the levels of no excess activity in Fig. 10. Although the data are meager the lethal levels bear a consistent relation to the levels of no excess activity throughout the whole of the biokinetic range. The fact that the lethal levels are lower than the levels of no excess activity would seem to indicate that the activity was not completely eliminated when the measurements of standard metabolism were made, the first of the two sources of error mentioned in the paragraph above. The level of no excess activity is therefore a conservative estimate of the lower limit to which the oxygen content can be reduced before it becomes too low for these speckled trout.

Under summer conditions when the fish are active, any drop in the oxygen content that is enough to reduce the maximum rate of oxygen uptake to any appreciable degree must be considered detrimental to the organism. However in winter when the call for activity is not so great, it may be possible for the speckled trout to live under conditions of oxygen that approach much more nearly to the lethal level. It is interesting therefore to note that the speckled trout can probably live in waters that have a considerable oxygen deficit in winter, at least where buffering is sufficient to prevent an undue rise in the free carbon dioxide. At 4° C. the level of no excess activity is 16% of air saturation (1.5 cc. per l.). The estimated lethal level at the same temperature is about 1 cc. per l. or 11% of air saturation. These estimates assume of course that no other harmful products of decomposition are present, but on the other hand they also make no allowance for acclimation to the gradually lowering oxygen content that would probably occur in nature.

Acknowledgments

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STUDIES OF WATERFOWL IN BRITISH COLUMBIA

BALDPATE[1]

BY J. A. MUNRO[2]

Abstract

A relatively large population of *Mareca americana* winters on the Coastal Plain, almost exclusively along the coast line when meadow flood ponds and sloughs farther inland are sealed by frost. A winter population in the interior is small in numbers and irregular in occurrence. Nesting grounds are in the interior only, from the Okanagan Valley and Kamloops-Nicola region, where the species is scarce, to as far north at least as the Haines Road in the northwest section of the Province. The most productive nesting grounds are in the Cariboo Parklands and the Lakes District near Vanderhoof. The main spring migration of transients through the central interior takes place during the last two weeks of April and by early May a breeding population is established on the many sloughs and ponds of the nesting range. Dry *Carex* meadows bordering certain water areas is the preferred nesting habitat. It is usual for the full clutch of eggs to be laid not later than June 15. In the Cariboo Parklands the average number of young in 10 June broods was 7.0, the average of 75 July broods was 6.2, and the average of 14 August broods was 5.2. In the Lakes District near Vanderhoof the average number of young in 37 broods during July and August was 7.0. Females with broods habitually frequent the open water of marsh ponds, lake bays, and marsh-edged rivers. Here, if approached by man, they vigorously defend their young by ruses to attract attention from them. Short, successive flights in front of a moving canoe, and splashing across the water in a direction leading away from the young are examples of behavior at this time. Postbreeding males associated in flocks on open water often accompany rafts of postbreeding coots and diving ducks. Aquatic insects is the chief item in the diet of downy young. Adults feed principally on the foliage of aquatic plants, grasses, algae, and seeds of aquatic plants, in that order. Insects are eaten in relatively small amounts. The baldpate may, under certain conditions and in certain localities, destroy cultivated forage plants. It is an important game duck and, because of its almost exclusive vegetable diet, highly palatable. Revenue derived from the hunting of baldpate, and the economic value of its flesh for human food, more than compensate for any economic loss resulting from crop destruction.

Introduction

In British Columbia the baldpate, *Mareca americana* (Gmelin), probably occupies fourth place in numerical status among the pond duck group of the Anseriformes. Winter populations occupy suitable habitat along the Pacific Coast from southeastern Alaska to Mexico, and in British Columbia a summer population is widely distributed through the central interior. It is not known to nest west of the Cascade and Coast mountain ranges. Recent information concerning the baldpate's breeding status in the Pacific States is lacking but apparently small numbers nest east of the Cascade mountain range as far south as Malheur Lake in southeastern Oregon and in Modoc County in northeastern California (3, 4).

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Contribution from Dominion Wildlife Service, Department of Mines and Resources, Ottawa, Canada.
[2] *Dominion Wildlife Officer for British Columbia.*

The facts of distribution, migration, and life history assembled in this paper represent the sum of field observations from 1911 to 1948, to which is added the small amount of data obtained from the banding of 306 baldpate, chiefly at Station 1 (See Table I). For explanation of the banding terms used see an earlier paper in this series (6).

TABLE I

NUMBER OF BALDPATE BANDED IN BRITISH COLUMBIA AND TOTAL RECOVERIES

Banding periods	Number banded			Totals	Totals recoveries	Recovery, %
	♂	♀	Not sexed			
Lulu Island						
1924, Mar. 15–Apr. 7	0	0	3	3	1	33.3
Station 1						
1928, Oct. 20–Dec. 1	1	0	0	1	0	
1930, Oct. 21–Dec. 5	0	1	0	1	0	
1931, Nov. 3–Dec. 9	3	6	0	9	0	
1932, Oct. 16–Dec. 9	11	16	0	27	5	18.5
1933, Mar. 29–Apr. 18	3	1	0	4	0	
1933, Oct. 4–Dec. 12	40	49	0	89	13	14.6
1934, Jan. 28–Mar. 14	6	7	0	13	2	15.3
1934, Oct. 7–Dec. 5	13	30	15	58	15	25.8
1935, Mar. 5–Apr. 11	0	0	0	0	0	
1935, Oct. 22–Dec. 31	0	6	0	6	0	
1936, Jan. 18–Apr. 11	0	1	0	1	0	
1936, Oct. 10–Dec. 28	2	4	0	6	1	16.6
1937, Mar. 19–Apr. 4	1	1	0	2	0	
1937, Oct. 31–Dec. 12	3	5	0	8	2	25.0
1938, Nov. –Dec. 31	0	0	22	22	2	9.1
1939, Jan. 1–Apr. 19	0	0	0	0	0	
1939, Nov. 14–Dec. 31	4	16	0	20	3	15.0
1940, Jan. 1–Mar. 31	10	10	0	20	0	
Station 2						
1933, Mar. 14–Mar. 29	3	1	0	4	0	
1934, Feb. 18	0	1	0	1	1	100.0
1935, " 11	0	1	0	1	0	
Station 5						
1933, Sept. 7–Oct. 6	0	0	10	10	1	10.0
Totals	100	156	50	306	46	

Total recoveries 15.03%

Distribution and Seasonal Movements

Coast Region

Autumn and Winter

Little precise information concerning autumn migration dates of the baldpate is available. The arrival of the main flights vary in time to a greater extent than do the flights of other pond ducks. In some years large numbers

have been recorded in November, as in 1938 when 500 were counted at Sooke Harbour, Vancouver Island, on Nov. 14.

In winter the British Columbia coast population is distributed from the Queen Charlotte Islands to Sooke Harbour and Esquimalt Harbour on the south end of Vancouver Island. Some of the many islands in Georgia Strait, the many inlets on the mainland coast, the Fraser Delta, the Pitt River region, and Boundary Bay are also populated to a greater or less degree. Part of the population appears to inhabit the sea littoral almost exclusively, another part uses sheltered bays of the sea chiefly as resting places and travels daily to feeding grounds on the fields, some of which are considerable distances inland. Other elements of the population are more or less sedentary on inland areas of the Coastal Plain but the size of these populations and their movements are modified in accordance with the amount of flood water on the fields. In dry years the numbers are small; in years of heavy precipitation the numbers may be large, but, as with other pond ducks, a sudden drop in temperature and consequent freezing of sloughs and flood ponds causes an immediate exodus of the population to the coast.

Selected winter counts are: Victoria Region, Jan. 5, 1940 – 266, Jan. 5, 1942 – 400 ±, Feb. 23, 1946 – 600 ±; Esquimalt Lagoon, Feb. 28, 1934 – 1000 ±; Comox, Dec. 20, 1925 – 300 ±; Westham Island, Dec. 4, 1934 – 800 ±.

More recent estimates of local winter populations, obtained during the January waterfowl inventory, follow:

	1947 Jan. 7 to 17	1948 Jan. 7 to 10	1949 Jan. 11 to 14
Fraser River mouth to Boundary Bay	7590	1060	3151
Southern Vancouver Island	4300	2055	4441
West Coast Vancouver Island	—	1800	—
Graham Island	300	100	400

From October, 1928, to Mar. 31, 1940, a total of 284 baldpate was banded at Station 1. Recoveries numbered 43, of which 33 represent birds shot, and 10 represent birds retrapped and released. Thirty-two are current recoveries from the Coastal Plain taken one day to three months after the date of banding and are distributed as follows: 17 at, or within a 12 mi. radius of, Station 1; one at Boundary Bay; eight at intermediate points; and six in Washington State from Sumas to Bellingham. Details of the remaining 11 recoveries of birds banded at Station 1, and three recoveries from birds banded elsewhere, are shown in Table II.

While it has seemed desirable to put these banding data on record the number of returns is not sufficient for detailed analysis. The high percentage of local current recoveries and the late dates on which they were recovered suggest that most of them represent baldpate that were wintering on the

TABLE II

RECOVERIES OF BALDPATE BANDED IN BRITISH COLUMBIA

Banding station	Date banded	Date recovered	Locality where recovered
Station 1	Nov. 20, 1932	Jan. 13, 1935	Jones Is., Haro Strait, B.C.
	Nov. 20, 1932	Jan. 30, 1934	Station 1
	Nov. 5, 1933	June 15, 1936	Fort Yukon, Alaska
	Nov. 5, 1933	Nov. 22, 1934	Skagit Co., Wash.
	Nov. 13, 1933	Nov. 30, 1934	Whatcom Co., Wash.
	Nov. 13, 1933	Jan. 1935	Sumas Prairie, B.C.
	Dec. 7, 1933	Nov. 2, 1934	Skagit Co., Wash.
	Jan. 30, 1934	Nov. 2, 1934	Skagit Co., Wash.
	Nov. 28, 1934	Dec. 3, 1935	Comox, V.I., B.C.
	Nov. 2, 1937	Dec. 4, 1938	Dewdney, B.C.
	Dec. 29, 1939	Dec. 10, 1940	Sardis, B.C.
Lulu Island	Apr. 2, 1934	Jan. 9, 1935	Lulu Island, B.C.
Station 2	Feb. 18, 1934	Oct. 4, 1935	Wembley, Alta.
Station 5	Oct. 6, 1933	Nov. 15, 1933	Skagit Co., Wash.

Coastal Plain. It will be noted that all autumn and winter recoveries in later years also are from the Coastal Plain, among them are one recaptured at Station 1, one shot at Sardis near Station 1, and one shot near Chilliwack about six miles distant.

Spring Migration

During late February and in March the winter population is increased by the arrival of transients from more southern latitudes. At this time disturbance to the normal activities of pond ducks caused by hunters has ceased so that many flooded fields adjacent to highways, which earlier in the season were avoided during daylight, now attract many pond ducks including baldpate (Fig. 1). Sample spring counts are: Somenos Lake, V.I., Mar. 3, 1939 – 300±; Quamichan Lake, V.I., Mar. 10, 1934 – 75; Victoria, V.I., Apr. 24, 1940 – 84; Boundary Bay, Mar. 23, 1922 – 750±, Mar. 15, 1934 – 200±. By the end of April the last of the spring flocks usually have migrated.

INTERIOR REGION

Winter

Baldpate winter irregularly, and usually in small numbers, in the Okanagan Valley and on the North Thompson River but not elsewhere in the interior so far as known. The small lakes and ponds that constitute their feeding grounds in spring and autumn are frozen even in mild winters; so also as a rule are the shallow margins of the large, deep lakes. Deprived through this circumstance of access to food by dipping, baldpate commonly frequent open water in the company of diving ducks and American coots, *Fulica americana*, and are largely dependent upon them for food. In another section of this paper the baldpate – diving duck relationship is discussed in some detail.

PLATE I

FIG. 1. *Baldpate on Quamichan Lake – Vancouver Island.*

Through the period 1911-1924 the population of baldpate wintering at the north end of Okanagan Lake was quite small, the largest number counted at any time being five observed frequently through January, 1918. More recently larger numbers have been recorded. Thus in the winter of 1938-39 when redhead, *Aythya americana*, and a smaller number of greater scaup duck, *Aythya marila*, wintered, a relatively large number of baldpate accompanied them through December and January at least. Precise counts are Dec. 28 – 160, Jan. 28 – 120. Observations were not continued beyond the last date so it was not learned what number, if any, remained through the balance of the winter. On Dec. 21, 1944, Swan Lake was frozen except for some 20 ac. on the east side; this open water attracted numerous diving ducks, and accompanying them on that date were 325± baldpate.

More recent observations made on Jan. 18, 1949, are of small numbers on the North Thompson River near Chase, viz.; four baldpate with 30 greater scaup duck, five with 250± greater scaup duck, and 26 in company with 20 mallard, *Anas platyrhynchos* (D. A. Munro in litt.).

Spring Migration

The spring migration of baldpate through the Okanagan, Nicola, and Kamloops regions takes place in late April, usually following the main flights of pintail, *Anas acuta*, and green-winged teal, *Anas carolinensis*. It is usual for them to travel in small flocks sometimes numbering 10 or less; the following are counts of some of the largest units tallied during the spring migration in recent years. Okanagan Lake, Mar. 28, 1939 – 39; Pond near Vernon, Apr. 18, 1939 – 40, Apr. 18, 1940 – 20, Apr. 18, 1941 – 21, Apr. 25, 1947 – 26; Rawlings Lake, Apr. 12, 1940 – 30. On certain lakes, used as feeding and resting places during migration, it is customary for a number of units to band together while they remain on these waters, as on a relatively large lake on the Vernon Commonage where 138 were counted in one flock on Apr. 16, 1948. Munson's Lake, near Kelowna, is another favored resting place where 400 were tallied on Apr. 23, 1938.

Observations of the spring migration in the Cariboo Parklands were made in April of 1940, 1941, and 1943. In the first year baldpate were not plentiful up to and including Apr. 24 when the study for the spring season was concluded. On that date the total tallied on two lakes was 37 and it was assumed that the main migration was still to come.

In 1941 during Apr. 15 to 17, the first three days of the study, only two flocks, each made up of 30 birds, were tallied. All of one flock, immobile on deep water 300 yd. from the shore of Lac la Hache, were obviously newly-arrived transients resting after a long journey. On Apr. 18 the transient population on the key lakes of the region had increased substantially, small flocks being sighted on most of the ponds and lakes visited. On Apr. 22 approximately 200, in units up to 40, alighted on 105 Mile Lake; on 149 Mile Lake a total of 80, and on Cummings Lake a total of 36, were counted.

In 1943 flocks containing a maximum of 40 individuals were counted in the Nicola Region on Apr. 27, at Clinton on Apr. 28, and at Lac la Hache on Apr. 30. The last had increased to 82 by 4.00 p.m. on that date. At Williams Lake at 11.30 a.m. on May 3, 20 birds in one flock were asleep on the water. The last, a flock of 20, to be identified as of the transient population, alighted on a pond near 103 Mile Lake on May 5.

Little information concerning the spring migration through the eastern interior is available. On the Kootenay Flats in early May, 1948, the few baldpate seen, viz.; May 10 – 4, May 15 – 8, May 17 – 4, were identified as late migrants; none are known to nest in the region.

Autumn Migration

An early southern flight of baldpate in the interior has frequently been observed. Thus, a flock of 200 ± was counted on a slough in the Lakes District near Vanderhoof on Aug. 22, 1945, and by the end of the month this flock numbered 400, approximately. Flocks totalling 150 were counted on a series of sloughs in the Okanagan Valley on Sept. 12, 1939, and 100 were counted at the same place on Sept. 12, 1940. The main migration takes place some time during October and November, with notable variation in time and in numbers. This irregularity is illustrated by the following estimates of maximum numbers tallied in each of 11 years at Swan Lake.

1933, Nov.	4 – 150	1943, Oct.	6 – 600
1934, Oct.	4 – 500	1944, "	30 – 200
1937, "	1 – 400	1945, "	10 – 30
1939, "	28 – 2500	1946, Nov.	13 – 225
1941, "	15 – 90	1948, "	13 – 1200
1942, Nov.	5 – 300		

On the Kootenay Flats in 1947 the first transients, a group of four, appeared on Aug. 12, and later arrivals were recorded as follows: Aug. 25 – 7, Aug. 26 – 500 ±, Sept. 10 – 50, Sept. 11 – 200 ±. In 1948 the tally of incoming transients was: Aug. 11 – 20 ±, Aug. 27 – 235, Aug. 28 – 275 ±, Sept. 16 – 120.

Reproduction

Two broods of baldpate counted at Swan Lake, Okanagan, July 31, 1940, and one brood observed at Hamilton Corrals in the Nicola District, Aug. 10, 1939, represent the most southerly breeding records in the Province. A brood of young seen at Mile 85 on the Haines Road is the most northerly one (T. N. Shortt, MS.). Relatively large populations inhabit the Cariboo Parklands (8), the Chilcotin Region (11), the Lakes District near Vanderhoof, where in 1945 it was the commonest nesting duck (10), and the Peace River Parklands, where in 1938 it outnumbered all nesting ducks except the mallard (2). Smaller populations have been studied on several lakes near Francois Lake and in lakes along the Bulkley River as far west as Smithers (9).

Baldpate arrive in the Cariboo Parklands during the latter part of April, some already being mated at the time of their first appearance on the lakes and sloughs of that region. For example, on Apr. 22, 1941, each of 8 or 10 mated pairs among several flocks of restless baldpate were conspicuous by reason of their relative immobility and constant close companionship. By the first week in May all but a few of the transients have left; the nesting population is assembled in small flocks, and there is much excited activity among them. It is common to see one or more males on the wing, in pursuit of a female, circle the pond that is their temporary home, and, after a short flight, drop to the water again. Nuptial flights of mated pairs around pond or slough also take place at this time. In the air the female utters a soft call-note, repeated numerous times in quick succession—a note identical in quality and volume to the alarm note given when a female is concerned about the safety of her young. The whistle of the male is also heard during the nuptial flights. Where a number of pairs are in joint possession of a pond they maintain fairly close association with one another and assemble in a flock when danger threatens. None seem to frequent or defend any particular feeding and loafing territory. By the first week in June the nesting population is widely distributed and the majority of females are either laying or incubating.

In the Lakes District, Vanderhoof, during the mating season of 1945 males outnumbered females and it was common to see groups of three or four males and one or two females circling the marshes. Sometimes females were accompanied by three or four males and mated pairs in courtship flight were joined by a second male.

Nesting

Baldpate seem to show preference—perhaps a group tradition—for nesting beside certain lakes while avoiding others in the same locality that have almost identical cover and food. For example, the species nests, sometimes commonly, at 103 Mile Lake but none do so at the adjacent and similar 105 Mile Lake (8). The preferred habitat is one of marshy sloughs in the grasslands, the site usually is in the dry *Carex*, that, in such places, forms an outer belt of vegetation around the marsh proper.

A nest with eight eggs found at Sorensen Lake, June 4, 1941, was situated in a 30-ft. strip of cultivated brome grass between a ploughed field and a marshy lake shore, the site being a tall brome grass clump 10 ft. from the edge of the ploughing and 100 ft. from the edge of the marsh. The nest was constructed substantially of straw and a small amount of down, which was added to during the week following. On the several occasions on which the nest was visited, the female flushed at about 10 ft., fluttered low over the top of the grass for a few yards, then flew to the lake.

A nest at Cummings Lake built beside a flat rock on a dry, open slope, 20 ft. from the lake shore, which at this point was fringed with round-stem bulrush, measured 8 in. in diameter, and was partly concealed by a tall clump

of fine grass. A high rim of down surrounded the seven eggs that were within a day or so of hatching on July 17, 1948. When flushed from the nest the female alighted on the lake at a point about 40 yd. distant.

Two nests were examined in the Lakes District, Vanderhoof. The first, made of desiccated sedge stems and situated among sedges 60 yd. from the edge of a marsh, contained eight eggs that were destroyed by crows prior to June 17 (1945). The second, concealed in thick vegetation near the margin of a brush-edged stream, contained eight eggs on June 13 (1946). This nesting was successful.

Brood Survival

Investigations of baldpate nesting populations in the Cariboo Parklands were carried on in each of the years from 1936 to 1943 with the exception of 1940. During this period a total of 99 females accompanied by broods was tabulated. The earliest date for the appearance of downy young was June 18, 1941; the average number of young in 10 broods counted in June was 7.0, the average number in 75 July broods was 6.2, and the average number in 14 August broods was 5.2.

In the Lakes District, near Vanderhoof, in 1945, the earliest date for the appearance of downy young was July 4; the average number of young in 37 broods counted through July and August was 7.0; in 1946 the average number in eight broods was 6.6; the earliest date for downy young was July 3.

In the summer of 1948 a Provincial Game Commission party working in the Chilcotin Region reported a total of 26 broods counted between July 5 and July 21 in which the average number was 6.7 (11).

At Francois Lake in August, 1944, the average number of young in four broods was 5.3; a larger number of young was associated with females in a single band that totalled 70. In July, 1946, the average number in five broods was 6.6.

In the Bulkley Valley, at La Croix Lake and Covert Lake, July, 1944, the average number in five broods was 7.0, and in a backwater of the Bulkley River near Smithers, July 17, 1944, a female accompanied a brood of 10.

Behavior of Females with Young

Female baldpate with broods of young are given to frequenting open water and it is common to see them swimming along the marshy edges of lakes and rivers. As in studying certain waterfowl it often is desirable to paddle a canoe along the margin of whatever waters are being investigated, this procedure afforded many opportunities to observe the fear reaction of the female baldpate in the presence of man. Their behavior under these conditions follows the same general pattern. Usually the duck will rise when the canoe is sighted, fly for a short distance over the water, then turn inshore and alight close to the canoe. Should the canoe be kept in motion the duck quickly takes wing again and, in a succession of short flights with intervening periods on the water, attends the progress of the canoe. A soft alarm note is

uttered frequently. Meanwhile the young, if they happened to be outside the marsh cover when the female left them, scamper over the water or swim less hurriedly to the shelter of the adjacent marsh. This behavior of the female has been observed when a brood was visible and when a brood was hiding in thick cover. In some instances when the brood was in plain sight on the water the female rushed across the surface for a short distance, with neck extended horizontally and wings threshing the water, before beginning the succession of short flights in the manner described. Occasionally also one will rejoin her brood after a demonstration of this sort that has continued but for a few minutes. More often, however, she will remain in the vicinity of the canoe. On one occasion, Williams Lake, Aug. 2, 1937, one continued the successive flights for two hours while a canoe was being paddled around the two mile circumference of a marshy bay. At the same place, on July 26, 1943, a female that had her brood hidden in the shore-lined marsh flew out and circled the canoe, then alighted on the water close by. As I paddled on she followed, or preceded, the canoe in a series of short flights and called continually. About one quarter-mile farther on a second female flew out of the marsh to join the first and behaved in the same manner. The two remained together and followed the familiar pattern of behavior for the next half-hour. Many similar instances could be cited.

Occasional departures from this common behavior have been observed. Thus, at 103 Mile Lake, July 18, 1939, where two females were leading their combined broods, one demonstrated in the usual manner while the other led the 18 young into the nearby bulrush marsh. Another female, which when first seen was swimming several hundred yards away from her brood of eight, took wing, circled the canoe several times, then dropped to the water. A moment later she flew directly to the young and led them into the marsh. In the Lakes District near Vanderhoof the banding together of several females and their broods was noted frequently, for example, on July 24, 1945, when one band of five females and 38 young, and another two females and 16 young were counted.

On Cummings Lake, June 30, 1942, a brood of eight young about one-fifth grown rushed out from the marshy shore to open water; the female, swimming about 30 yd. away, rose at once and, dropping again to the water immediately behind the young, urged them forward by rushing back and forth across the surface, sometimes standing upright and splashing with her wings. At 103 Mile Lake, July 12, 1942, a female with three large young acted in an identical manner. At the same lake a little later a small downy baldpate swam out from the rushes, joined a brood of three buffle-heads and with them swam off behind the foster mother. On Nulki Lake, near Vanderhoof, a quite different behavior was general; it was usual for the female to swim ahead of the brood and, if pressed, lead them in a rush across the water toward cover on shore (10).

Females accompany their broods until the young are nearly full-grown, sometimes after they have reached the flying stage. No information concerning the flightless period of the female has been obtained other than the obvious fact that the flying stage occurs some weeks later than it does with males.

Postbreeding Behavior of Males

Most of the females are incubating by the third week in June and the males have left them. The latest dates on which mated pairs were observed are June 22, 1941, and June 21, 1945. Some males associate in small bands that may include a few females, presumably those that for one reason or another have failed to mate or that have nested unsuccessfully. As both males and females are sexually mature in their second year the number of nonbreeding birds in any population is not large. Other males, in this early midsummer season, associate with postbreeding mallard and pintail and may continue to do so for several weeks. Still others band together in much larger flocks that may join rafts of postbreeding diving ducks on open water. Early records for flocks of postbreeding males are: Elliot Lake, June 12, 1942 – 18; 103 Mile Lake, June 16, 1942 – 5. By the first week in August the majority, in full or partial eclipse, are flightless – a condition that lasts about three weeks.

The number of postbreeding males present on any particular series of sloughs does not necessarily indicate the size of the local nesting population as there is considerable movement from one district to another. Thus at Minnie Lake, situated in the Nicola Region, where a few baldpate nest, a total of 60 males was counted on Aug. 10, 1938. Other instances of a southern movement of postbreeding males have been noted. How far south these movements extend is not known.

The fluctuation in numbers from year to year, so apparent in transient flocks and winter populations composed of both sexes, is noted also in the postbreeding flocks of males on the nesting grounds. For example, in the Cariboo Parklands considerably more postbreeding males were tallied in 1937 and 1939 than during the three succeeding summers.

The following table of enumeration shows the periods in which postbreeding males are most conspicuous, and the variation in size of flocks.

Flightless males in eclipse seem less inclined to seek concealment than do the males of other pond ducks when in this condition and are frequently prominent in rafts of postbreeding diving ducks. When alarmed they flap across the water sometimes to a distant part of the lake, sometimes to cover along shore. They have not been seen diving to escape pursuit as diving ducks commonly do.

At Williams Lake, Aug. 2, 1937, when a flock of 80 baldpate, strung out on shallow water along the edge of a marshy bay, were approached from the open lake they became uneasy and swam toward an adjacent part of the shore where willows overhung a low bank. Becoming alarmed more as the result of a closer approach most of them rushed over the water with a great deal of

Cariboo Parklands			
Slough, 1 ac.	Aug. 2, 1937	4	
Slough, 20 ac.	" 2, "	10	
Williams Lake	" 2, "	81	
149 Mile Lake	" 2, "	8	
103 Mile Lake	" 4, "	130	
105 Mile Lake	" 6, "	7	
Elliot Lake	" 7, "	25	
Lily Pad Lake	" 7, "	9	
Lily Pad Lake	July 6, 1938	6	
Westwick Lake	" 9, "	71	
Slough, 5 ac.	" 13, "	2	
Slough, 2 ac.	" 13, "	5	
Elliot Lake	" 19, "	4	
Murphy Lake	July 15, 1938	40	
Lakes District, Vanderhoof	June 16, 1945	50±	including a few females
	" 23, "	23	
	July 4, "	80±	
	" 15, "	100±	
	" 24, "	300±	

splashing toward the main lake. A few rose, but with difficulty, and were able to fly only a short distance after which they dropped to the water again. Two birds that were left behind fluttered along the shore for a few yards then climbed the bank and disappeared in the brush.

At 103 Mile Lake, Aug. 4, 1937, approximately 100 eclipse males accompanied a raft of diving ducks. When approached they flapped across the open water at a high rate of speed; none dived as did a few adolescents that were with them. On Aug. 20 the number of flightless males on this lake was reduced to approximately 50 and on Aug. 25 none were seen there.

Food and Feeding Habits

In British Columbia baldpate feed upon the foliage and stems of aquatic plants to a greater extent that does any other pond duck with the possible exception of the gadwall, *Anas streperus*. This fact is reflected in the size of the gizzard and the character of the abrasive material ingested to help macerate the food. It has been observed that a correlation exists between the type of food eaten by different species of pond ducks and the size of the gizzard. Species that eat chiefly bulky foods have larger gizzards in proportion to their size than do those that habitually eat more concentrated foods. Thus the gizzard of the baldpate is large in proportion to the bird's size and weight. The abrasive ingested is almost invariably a fine sand, rarely coarse sand, and never gravel. Gizzards of green-winged teal, mallard, and pintail, species that eat many molluscs and crustaceans, invariably contain relatively large amounts of gravel. The vegetation in the gizzards of baldpates frequently is comminuted and thoroughly mixed with sand so that identification of the plants eaten is difficult or impossible.

On the nesting grounds baldpate obtain much of their food by dipping in the shallows and by surface feeding; on migration they associate with diving ducks and American coots and obtain no small proportion of their daily food by robbing the diving birds of the vegetation they bring to the surface. This habit, considered to be of great importance in the life of the baldpate, is discussed more fully later.

Forest ponds and water holes, which in late summer are completely covered with duckweed, *Lemna minor*, are attractive feeding places and this small plant is eaten extensively.

On the Fraser Delta, baldpate, sometimes in company with other pond ducks, visit cultivated meadows and feed on the fresh green forage plants; clover is particularly attractive to them. When fields are partly flooded, which they sometimes are from November to April, the ducks may concentrate on the flood ponds and their constant feeding, which involves pulling up grass plants by the roots, may result in partial destruction of the crop on these particular areas, so that when waters recede in spring the former flood ponds appear as dark patches among the prevailing green vegetation. During the hunting season feeding is done mostly at night. At times when snow covers the ground baldpate have been seen in rural vegetable gardens feeding on Brussels sprouts or whatever other leafy plants are accessible above the snow. Flocks frequent the golf links on southern Vancouver Island, the extensive lawns of Beacon Hill near Victoria and other similar open territory where green food is available even in the coldest weather. At the last place it is not unusual to see several flocks containing 50 birds and more pasturing the green grass. The smaller isolated islands in Georgia Strait, because of the food to be found there and because comparative safety from hunters is assured, also are attractive to them. Thus Snake Island near Departure Bay, which contains patches of green turf and chickweed between thickets of salal and tall rye grass, is visited frequently.

Along the sea beaches of Vancouver Island and elsewhere, sea lettuce, *Ulva* sp., and other algae are eaten; some baldpate populations appear to live on this food almost exclusively for weeks at a time, avoiding the various small animals such as gastropods and crustaceans, which generally are associated with the algae. On a falling tide the ducks may be seen following the receding waters and pulling up algae as rapidly decreasing depths bring it within their reach.

The commensal relationship with diving ducks and coots referred to earlier in this paper has been noted by several authors who are quoted by Bent (1). When baldpate are associated with a flock of diving ducks they swim quickly from one to another of the birds that have just risen to the surface, and should one have plant material pendent from its bill a baldpate will attempt to snatch it. It is a scene of confused activity as the baldpate weave in and out among the other ducks or make short flights from one section of the flock to another. There are the accompanying noises of constant splashing and the characteristic

whistled calls of the males. The ducks from whom food is taken do not resent the robbery by any aggressive action. In addition to the food obtained by this means baldpate also pick up some of the plant foliage that has become detached and risen to the surface, and on the surplus material dropped by the diving birds—representing a considerable amount when a large flock is actively feeding.

The robbery method of obtaining food is more general than the literature on the subject would indicate. In the interior it has been observed as a constant habit not only in winter, when it is necessary to survival because shoal-water feeding grounds are frozen, but in the autumn when baldpate can obtain abundant food in the conventional manner of feeding. Thus at Swan Lake, Okanagan, baldpate habitually associate with coots on relatively deep water and subsist almost entirely on *Chara*, which the coots bring to the surface.

There is evidence also that baldpate accompany, or follow closely, the autumn migrations of diving ducks. For example, at Swan Lake, Okanagan, on Oct. 6, 1943, flocks of baldpate and redhead, flying separately, arrived between 11.30 a.m. and 12.30 p.m.

So also in spring large numbers of baldpate associate with flocks of lesser scaup duck and other diving ducks. In the Lakes District near Vanderhoof flocks up to 30 attended the diving operations of mixed flocks of diving ducks, of coots, and once, May 1, 1945, were observed with a flock of whistling swan, *Cygnus columbianus*, on the Nechâco River.

Postbreeding diving ducks that raft on certain lakes in the Cariboo Parklands are a potent attraction for baldpate. For example, at 103 Mile Lake, Aug. 4, 1937, over 100 males were scattered among a much larger number of lesser scaup duck, canvas-back, and other species. Through the summer similar associations involving smaller numbers are observed frequently. Thus at 103 Mile Lake on Aug. 6, 1940, four adult males, several adult females, and 20 young of different ages accompanied a flock of diving ducks, chiefly lesser scaup duck. At 150 Mile Lake, Aug. 10, 1940, four young baldpate, nearly full-grown, were attached to a band of lesser scaup duck that included both adults and young. At Swan Lake, Okanagan, June 4, 1938, eight baldpate were attached to a flock of 19 redhead and when disturbed all flew off together.

The amount of food obtained by baldpate in summer through association with diving ducks is much less than the amounts obtained in autumn and winter, the reason being that in summer animal food such as amphipods and aquatic insects predominate in the diet of diving ducks and these small objects are swallowed while the feeding duck is submerged. Nevertheless the association persists.

Commensal association begins soon after the young are hatched and it is common to see female baldpate with small young attached to flocks of diving ducks. It has been observed also numerous times that baldpate broods are

met with more often on the open water of ponds and lakes than in marsh or brush cover, a habitat preference in marked contrast to the preference of other pond ducks for concealing cover. It is suggested that two characteristic baldpate habits, viz.: commensal association with diving ducks and coots, and preference for an open water habitat, reacting constantly one on the other have developed concurrently to make the species unique among pond ducks in these respects.

The stomach contents of 65 baldpate, comprising 15 adult specimens from the Coast Region, one from Alta Lake, 38 adults, one juvenile, and 10 downy young from the Interior Region, are summarized in the following paragraphs.

Food of Downy Young

The food of 10 downy young consisted of 87.80% animal matter, chiefly insects, and 12.20% vegetation. Three taken at Bradley's Slough, 12 mi. south of Vanderhoof, on July 16, 1945, contained insects in the following percentages of total volume, viz.: 100, 90, 60, the additional food being leech egg cases in one, and *Carex* seeds with vegetable debris in the other. The insects identified were damselfly and dragonfly nymphs, aquatic beetles, both adults and larvae, and midge larvae.

Three from a small slough at Springhouse, Cariboo Parklands, June 20, 1941 – 2, July 7, 1941 – 1, contained 100%, 98%, and 75%, respectively of insect material including mayfly nymphs, aquatic beetle larvae, corixids, and adult and larval midges; a few seeds of *Potamogeton pectinatus* and *Scirpus acutus* also had been eaten.

One collected at Cummings Lake, Cariboo Parklands, June 22, 1943, had eaten damselfly nymphs, corixids, midge adults, and pupae, as well as a few *Sparganium* seeds and leech egg cases, the insect material composing 90% of the total food in the stomach.

One specimen from Williams Lake, Cariboo Parklands, July 4, 1938, contained 90% miscellaneous vegetable matter and 10% insect debris.

Two collected at Tupper Creek, Peace River Parklands, contained respectively 100% and 89% insect material consisting of midge pupae (*Ceratopogonidae*), midge larvae (*Chaoborus* sp.), dragonfly nymphs, corixids, and terrestrial coleopterans. The remaining food items were cladoceran egg cases, one *Carex* seed, and a trace of algae.

Food of Juvenile

The stomach of a juvenile, about one-half grown, collected at 103 Mile Lake, Cariboo Parklands, Aug. 4, 1948, was filled with comminuted grass fibers; two seeds of *Potamogeton pusillus*, and one seed of *Myriophyllum spicatum* together represented less than 1% of the food present.

Food of Adults, Interior Region

The food of 38 adults consisted of 5.75% animal matter, chiefly insects, 29.35% algae, and 64.87% vegetation.

FOOD OF 10 BALDPATE, DOWNY YOUNG; PERCENTAGE OF TOTAL VOLUME

Localities and number of specimens		Crustaceans	Odonata	Corixids	Chironomids	Coleoptera	Misc. insects	Seeds	Misc. vegetation
Bradley's Slough	3	—	26.67	—	15.00	30.00	10.00	5.00	—
Slough Springhouse	3	—	—	9.34	8.33	33.34	40.00	2.33	6.66
Cummings Lake	1	—	20.00	5.00	65.00	—	5.00	5.00	—
Williams Lake	1	—	—	—	—	—	10.00	—	90.00
Tupper Creek	2	5.00	5.00	—	67.00	22.33	—	0.67	—

Animal food 87.80%; Vegetable food 12.20%

A specimen from Irish Lake, Sept. 25, 1940, contained comminuted plant foliage exclusively; in another taken at the same place, Oct. 14, 1940, were pieces of a rush, *Juncus* sp., 100%; two seeds of *Carex* sp. and one of *Scirpus acutus* represented less than 1% of the stomach contents.

One from Disputed Lake, Sept. 23, 1940, had eaten several hundred mosquito larvae, *Culex* sp., as well as corixids and 100+ bryozoan statoblasts.

One collected on a small lake near 108 Mile, Oct. 20, 1940, contained 99% miscellaneous plant material including *Lemna minor*, a few seeds of *Scirpus acutus* constituting the remaining 1%.

The three localities referred to are in the Cariboo Parklands.

A specimen from Alta Lake, 37 mi. north of Squamish, Sept. 30, 1944, contained stems and leaves of grass exclusively, and one from the north end of Okanagan Lake, Nov. 17, 1939, was filled with *Elodea canadensis*, the sole item.

The contents of 33 stomachs from Swan Lake, Okanagan, September – 5, October – 22, November – 5, December – 1, are summarized as follows: aquatic vegetation, usually comminuted and mixed with sand, was the sole or major item in 21 stomachs. Plants identified were *Potamogeton pectinatus*, *Potamogeton* sp., *Utricularia* sp., and *Ceratophyllum demersum*. Next in importance were the branches of *Chara* sp., which constituted the exclusive item in seven, and 99% and 94% of the total food in two others. Seeds of *Scirpus acutus* was the sole food in one, 85%, 70%, 50%, 50%, and 25% in five, and represented minor amounts in three other stomachs. Seeds of other aquatic plants eaten were *Potamogeton pectinatus*, *Polygonum Muhlenbergii*, and *Rumex maritimus* (fruits). These seeds were present in small quantities, as were *Chara* oöspores and an unidentified alga. One bird had eaten a bristle-worm, *Nais* sp., another approximately 50 corixids, and a trace of this insect was found in a third specimen.

Food of Adults, Coast Region

Eighteen stomachs of baldpate from the Coast Region represent the following localities, viz.: Sardis, November – 1; Pitt Meadows, December – 1; Nicomen Island, November – 1; Boundary Bay, March – 3; Ione Island,

TABLE III

FREQUENCY OCCURRENCE OF FOOD ITEMS IN 65 BALDPATE STOMACHS

Bryozoa	Statoblasts	1
Bristleworm, *Nais* sp.		1
Leech, Hirudineae	Egg cases	2
Water flea, Cladocera	Egg cases	1
Mayflies, Plectoptera	Nymph	2
Damselflies, Odonata	Nymph	3
Dragonflies, Odonata	Nymph	2
Water boatman, Corixidae	Adult	7
Beetle, terrestrial	Adult	5
Beetle, aquatic	Adult	2
Beetle, aquatic	Larva	2
Midge, Chironomidae	Adult	3
Midge, Chironomidae	Larva	3
Midge, Ceratopogonidae	Pupa	2
Midge, *Caorbornis* sp.	Larva	2
Mosquito, *Culex* sp.	Larva	1
Fly, Diptera	Pupa	1
Ant, *Formica lufa melanotica*	Adult	1
Insect debris, unidentified forms		5
Muskgrass, *Chara* sp.	Branches	9
Muskgrass, *Chara* sp.	Oöspores	2
Algae, unidentified freshwater form		2
Algae, unidentified marine form		2
Algae, sea lettuce, *Ulva* sp.		3
Bur-reed, *Sparganium* sp.	Seeds	2
Pondweeds, *Potamogeton* sp.	Foliage	2
Potamogeton pusillus	Seeds	1
Potamogeton pectinatus	Foliage	2
Potamogeton pectinatus	Seeds	3
Water plantain, *Alisma plantago aquatica*	Seeds	1
Water weed, *Anacharis canadensis*	Foliage	1
Grass, Gramineae	Leaves	12
Grass	Seeds	1
Tall hair grass, *Deschampsia caepitosa*	Seeds	1
Sedge, *Carex* sp.	Seeds	5
Sedge, *Carex Barbareae*	Seeds	1
Sedge, *Carex arcta*	Seeds	1
Bulrush, *Scirpus acutus*	Seeds	11
Scirpus americanus	Seeds	1
Spike rush, *Eleocharis palustris*	Seeds	1
Rush, *Juncus* sp.	Stems	1
Duckweed, *Lemna minor*		1
Dock, *Rumex maritima*	Fruits	1
Water smartweed, *Polygonum Muhlenbergii*	Seeds	1
Water buttercup, *Ranunculus* sp.	Seeds	1
Cinquefoil, *Potentilla montspeliensis*	Seeds	1
Clover, *Trifolium* sp.	Leaves	1
Water milfoil, *Myriophyllum spicatum*	Seeds	1
Hornwort, *Ceratophyllum demersum*	Foliage	1
Bladderwort, *Utricularia* sp.	Foliage	1
Unidentified plant debris	Foliage, stems	20

November – 1; Lulu Island, November – 1; Albert Head, January – 1; Nanaimo Flats, December – 1; Departure Bay, December – 1; Snake Island, near Departure Bay, January – 1; Quennell Lake, January – 1; Comox, March – 2. The six localities last named are on Vancouver Island.

One specimen from each of the localities Albert Head, Nanaimo Flats, and Quennell Lake contained grass leaves and fibers exclusively. The sole item

TABLE IV

FOOD OF 54 ADULT BALDPATE, PERCENTAGE OF TOTAL VOLUME

Locality and number of specimens		Insects, other inverte-brates	Chara	Other algae	*Scirpus* seeds	Other seeds	Grass	Foliage aquatic plants
108 Mile Ranch	1	—	—	—	1.00	—	—	99.00
Irish Lake	2	—	—	—	—	—	—	100.00
Disputed Lake	1	100.00	—	—	—	—	—	—
Okanagan Lake	1	—	—	—	—	—	—	100.00
Swan Lake, Okanagan	33	1.16	27.19	1.07	10.25	1.39	3.03	55.91
Alta Lake	1	—	—	—	—	—	100.00	—
Boundary Bay	3	—	—	—	—	—	100.00	—
Sardis	1	—	—	—	—	50.00	50.00	—
Nicomen Island	1	2.00	—	—	—	1.00	—	97.00
Ione Island	1	—	—	—	—	—	100.00	—
Lulu Island	1	—	—	100.00	—	—	—	—
Pitt Meadows	1	1.00	—	—	—	99.00	—	—
Nanaimo Flats	1	—	—	—	—	—	100.00	—
Departure Bay	1	—	—	100.00	—	—	—	—
Snake Island	1	—	—	100.00	—	—	—	—
Quennell Lake	1	—	—	—	—	—	100.00	—
Comox	2	—	—	100.00	—	—	—	—
Albert Head	1	—	—	100.00	—	—	—	—

in two from Comox and one from Departure Bay was sea lettuce, *Ulva* sp., and one from Snake Island contained an unidentified marine alga only.

Three collected in a hay field at Boundary Bay, Mar. 24, 1922, had eaten new grass shoots some with roots attached, and one stomach contained a few clover leaves, *Trifolium* sp.

The stomach of a specimen from Sardis, Nov. 20, 1934, held equal amounts of grass leaves and seeds of *Sparganium* sp.

Grass fragments represented 99% of the contents of one from Nicomen Island, in the Lower Fraser River, Nov. 4, 1934, the remaining small quantity of food present being *Eleocharis palustris* seeds and corixid debris.

One specimen from Ione Island in the mouth of the Fraser River, Dec. 29, 1941, contained grass leaves and four seeds of *Scirpus americanus.*

The sole food item in one from Lulu Island, Nov. 10, 1946, was a marine alga.

Seeds of aquatic plants constituted 99% of the food in a specimen from Pitt Meadows, Dec. 16, 1923, the species represented being: sedge, *Carex Barbareae* and *C. arcta*, hair grass, *Deschampsia caespitosa*, and cinquefoil, *Potentilla monspeliensis.* Eight pupae of a fly and the head of a terrestrial beetle composed the remaining one per cent.

Food Summary

The food of 10 downy young collected in the Cariboo Parklands, the Peace River Parklands, and the Vanderhoof Region was composed chiefly of aquatic

insects, the most prominent items being chironomid larvae and Odonata nymphs. Miscellaneous vegetation was the chief food eaten by one half-grown young, and the seeds of aquatic plants were present in three stomachs. In the diet of adults the foliage of aquatic plants was first, grasses second, and algae third in times of occurrence and percentage volume. Seeds of aquatic plants were less often represented, and animal matter, chiefly insects, was of minor importance, the total percentage volume being only 5.75%.

Economic Status

In the winter and spring baldpate cause damage to agricultural crops in the Lower Fraser Valley by concentrating on shallow flood ponds that have formed in the fields and by feeding on young forage plants growing there. Damage to fall-sown grains also occurs when the young plants are small. The habit is a local one, the damage caused is not usually serious and is amenable to control. Damage to vegetable crops, particularly lettuce, so common a cause for complaint in the southwestern United States, and providing a problem in game management that so far has not been resolved, is of slight importance in British Columbia. The value of the species as a game bird, and for food, would seem to more than balance the loss suffered by agriculture in British Columbia. This duck does not eat salmon eggs or the flesh of spent salmon, and rarely if ever eats marine crustaceans or molluscs – foods that taint the flesh and that are commonly eaten by mallards and some other duck species wintering on the coast. Consequently the baldpate is esteemed as a table bird.

Acknowledgments

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